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Introduction

In view of the steadily increasing interest in the chimpanzee and its use in experimental procedures for which animals of a lower order are undesirable, it is necessary that the fundamental features of this animal's physiology be examined. From the standpoint of comparative physiology such a study is particularly essential because anatomically and physiologically this primate is more nearly similar to man than any other animal. One of the major aspects of the physiology of the chimpanzee is its respiratory metabolism. A decade or more ago, Professor Robert M. Yerkes and one of us (F.G.B.) discussed on several occasions the importance and possibility of making a metabolic survey of this animal. In physiological comparisons of animals of different species a complete study of one animal of any given species may possibly be justified, especially when this particular animal is in the lower order of the zoological scale and when the technical difficulty in such a study practically precludes an exhaustive survey. The original thesis of the Nutrition Laboratory has been that the value of any metabolic study of an animal depends not only upon the extent to which it contributes information to comparative physiology in general, but more particularly upon the extent to which it illuminates studies in human physiology. Obviously, therefore, in an investigation with an animal so closely approximating the human as does the chimpanzee a casual survey of its metabolism would be scientifically dishonest and unjustifiable. Because at the time of the original conference with Professor Yerkes no appreciable number of chimpanzees

was available, it was decided that the study should be postponed until the plan (then being considered by Professor Yerkes—1916) for collecting, housing, and breeding a relatively large group of these animals materialized.

In 1931 the Carnegie Institution of Washington initiated a cooperative research by its Department of Embryology and its Nutrition Laboratory to study the respiratory metabolism of the macaques in the collection of Dr. George L. Streeter at Baltimore, Md., an investigation which is still in progress. Later the junior author (Bruhn, 1934) measured the respiratory exchange of the three chimpanzees in the laboratory of the Department of Physiology at Yale University.[1] The macaques at Baltimore proved to be extremely intractable and it was difficult to obtain periods of complete muscular repose. The experience at New Haven was much different, for quiet periods of measurement were secured there, not only with the macaques but also with the chimpanzees. Before any extensive study of the chimpanzee was undertaken, therefore, reasonable assurance was obtained that this animal would prove to be a better subject for metabolism studies than the macaque because of its relatively more stable nervous mechanism.

Due principally to the well-directed efforts of Professor Yerkes and his staff a large and excellent group of chimpanzees was finally collected or reared at the Yale Anthropoid Experiment Station at Orange Park, Florida. Consequently it seemed that the time had arrived for a survey of the metabolic characteristics of the chimpanzee, to supplement the previously initiated study of the metabolism of the *Macacus rhesus* by the Carnegie Institution of Washington and to add one more animal to the many already chosen by the Nutrition Laboratory for intensive study. In fulfillment of this Laboratory's comprehensive program of research, observations had already been made on both poikilotherms and homoiotherms. The cold-blooded animals ranged in size from small snakes of from 5 to 15 kg. to a 32-kg. python, a 53-kg. alligator, and a 132-kg. tortoise, and the warm-blooded, among the birds, from the 20-gram canary to the 17-kg. cassowary and among the mammals from the 20-gram mouse to the 4,000-kg. elephant. This contemplated survey of the chimpanzee was likewise to further the purpose of the Yale Laboratories of Primate Biology, Inc., to collect information (psychological, anatomical, and physiological) regarding the chimpanzee which would make it increasingly available and useful

[1] The literature contains no data on the respiratory metabolism of the chimpanzee, other than the observations published by Bruhn.

as a laboratory animal. Inasmuch as the desires of both laboratories were sufficiently identical at the start of the proposed survey, the facilities of the Nutrition Laboratory and the Yale Laboratory were combined to avoid duplication of effort and expense. Therefore, in the spring of 1933 plans were made for a cooperative study of the respiratory metabolism of the chimpanzee. The Department of Physiology of the School of Medicine of Yale University, through Professor John F. Fulton, manifested a continued interest in the project and supplied a Sterling Fellowship for the junior author for the year 1933–34. The Orange Park laboratory provided laboratory facilities, placed at our disposal the entire colony of chimpanzees, the individual records of the animals, and contributed importantly from its knowledge of chimpanzees to the problem of handling these powerful and potentially dangerous animals. At the end of the year 1933–34 the Orange Park laboratory assumed a relatively greater amount of responsibility for and costs of the investigation by making one of us (J.M.B.) a member of the station staff.

Plan of research

The experiments were formally started on the first of November 1933. After a few preliminary observations on adult, female chimpanzees weighing from 30 to 40 kg., it was decided desirable and practical to make a metabolic survey of all the available adults. Early in 1934 arrangements were completed that allowed the work to be continued until July 1935. This modified the original plan so as to include one adult male and several adult females, as well as adolescents and infants (1 year old) of both sexes as they were weaned from their mothers. The particular subjects of investigation were the respiratory quotient as an index of the post-absorptive state, the variability in metabolism from day to day, the metabolic effects of such factors as muscular activity, training, emotional excitement, sleep, individuality, environmental temperature, and season, and particularly the effects of age, size, sex, and the menstrual cycle.

Animals used

The group of chimpanzees at Orange Park is primarily a breeding colony and as such is unique both in the number of animals and in the completeness of the individual histories. A few of the chimpanzees were captured in Africa and brought to the Florida Station. Others were obtained as a result of a gift from Mr. Pierre S. Abreu of Havana, Cuba. Still others were born in captivity, and knowledge is available regarding the exact ages, development, and parentage of these animals.

Living conditions

Housing.—The chimpanzees are housed in large outdoor living quarters (Yerkes, 1932) which have connections with inside rooms maintained at 20° C. during the cold weather. A roof over a portion of the outside cage protects the animals from sun or rain if they so desire. A sliding door, which the animals can operate, serves to close off the warm living rooms from the outside. In a sense, therefore, the chimpanzee is free to choose its environmental temperature. The buildings are constructed of concrete and steel. The floors are an asphalt composition. Such an arrangement of cages makes for the safety, cleanliness, and comfort of the animals.

Social aspects.—Emphasis is placed upon the social aspects of the chimpanzee's life. Animals are given one or more cage mates with whom they are congenial. Usually males are caged alone, except for mating at specified times. On the whole, the animals are friendly and cooperate with the observers and caretakers, although one does not enter the cages of the adults except for special reasons. Because of the attention given to the congeniality of the cage mates there is a minimum amount of battling with enemies.

Climate.—The type of housing provides plenty of sunlight and outdoor air and offers protection against extreme temperature changes. The colony is located in northeastern Florida, not far from Jacksonville. The temperature seldom rises above 96° F. (35.6° C.) in the summer and seldom falls below 35° or 40° F. (1.7° or 4.4° C.) in the winter. At Jacksonville, 14 miles north of the station, the mean maximum for January (the coldest month) is 64.8° F. (18.2° C.) and the mean minimum 48.2° F. (9.0° C.). During August the mean maximum is 88.6° F. (31.4° C.) and the mean minimum 73.8° F. (23.2° C.). The mean relative humidity at Jacksonville in January at 7 a.m. is 86 per cent and at 7 p.m., 77 per cent. In August it is 85 and 81 per cent, respectively. The mean annual precipitation is 50.67 inches (129 cm.), November having the lowest (2.12 inches or 5.4 cm.), and September the highest (7.40 inches or 18.8 cm.). In January the precipitation averages 2.83 inches (7.19 cm.) and in August 6.04 inches (15.3 cm.). The average velocity of the wind is 8.5 m.p.h., and the prevailing winds are from the northeast (Mitchell and Ensign, 1928).

Feeding.—The chimpanzees are liberally and scientifically fed. Food preferences exist among them but not to the extent that formulation of a well-balanced diet for any individual is rendered difficult. The typical dietary for a 40-kg. chimpanzee allows an energy intake of

approximately 2,900 calories per day, made up from oranges or grapefruit and banana, white and sweet potatoes, cabbage or onion (raw), steamed beans with molasses, rutabaga, peanuts, milk, a cereal mixture of rolled oats and grits, tomatoes, and a "chimcracker" composed of graham flour, cracked wheat, corn meal, oatmeal, powdered whole milk, peanut butter, ground raisins, dark molasses, and bone ash. Not all of these foods are given on a single day. From time to time other seasonable foods such as carrots, celery, and peaches are given. Of the total daily energy intake of 2,900 calories about 12.3 per cent is derived from protein, 70.0 per cent from carbohydrates, and 17.7 per cent from fat. During the winter months cod liver oil (1 large tablespoonful twice a week, *i.e.*, 25 c.c.) is given directly from a spoon. The diet of the infants differs from that of the adults in that it contains a relatively greater amount of milk, cereal, and fruits. The calcium and phosphorus intake is well over the accepted minimum allowance for man. The amount of iron has recently been increased by using in the baking of the chimcrackers "black-strap" molasses, which is a good source of iron. The vitamine requirements are amply taken care of by the varied vegetable diet. At first sight this seemingly elaborate provision for a well-balanced diet might appear unnecessary, but the unique experience of this Florida colony in approximating perfect health, growth, and reproduction wholly justifies all these precautions to provide the captive chimpanzee with those subtle alimentary and medicinal properties found instinctively by the chimpanzee in its natural habitat.

Detailed description of each chimpanzee

Twenty-two of the thirty chimpanzees contained in the colony were used in the metabolism experiments. The physical characteristics of each are indicated in table 1, the animals being listed in the order of increasing age. The estimate as to the amount of hair on each chimpanzee represents a composite opinion of four members of the staff at Orange Park (Spragg, McCulloch, Elder, and Bruhn), 1 indicating the least hair and 4 the best coat of hair. The life histories of these animals are as follows:

Peter, born at Orange Park, is the son of Cuba (mother) and Bokar. His mother did not care for him properly, and eighteen hours after his birth he was taken away from her and fed evaporated milk according to formula. He throve from the start and is now (January 1936) a well-developed infant. On July 22, 1935, the last date at which he was studied, his diet consisted of evaporated milk according to formula, viosterol in halibut liver oil (250-D), banana and orange juice. A

statement about the birth and ancestral history of Peter has been given by Yerkes (1935).

Don, born at Orange Park, is the son of Nana (mother) and Pan. He became thin while with his mother and was separated from her when approximately 11 months old. He was eating well and drinking milk when used in metabolism experiments about 6 weeks after separation.

TABLE 1.

PHYSICAL CHARACTERISTICS OF CHIMPANZEES.

Name	Animal record No.	Date of birth	Sex	Estimated amount of hair[1]	Range in body weight while studied: Minimum	Range in body weight while studied: Maximum	Approximate Age: When first studied		Approximate Age: When last studied	
					kg.	kg.	yr.	mo.	yr.	mo.
Peter	41	April 11, 1935	M	3	2.94	3.85		2		3½
Don	39	May 2, 1934	M	3	4.80	5.08		11½		11½
Rosy	68	April 21, 1934	F	3	4.35	4.74		11½	1	
Dick	37	July 15, 1933	M	2	5.30	5.86	1	1	1	2
Bob	35	June 27, 1933	M	2	4.44	5.39	1	1½	1	2½
Helene	62	June 26, 1933	F	3	5.34	6.00	1	1½	1	2½
Tom	33	June 26, 1933	M	3	6.84	7.64	1	1½	1	2½
Ben	23	May 14, 1933	M	4	4.75	7.76	1		1	3½
Gamma	58	Sept. 21, 1932	F	4	6.69	12.0	1	5½	2	9
Beta	52	Oct. 31, 1931	F	3	8.94	14.2	2	4½	3	6
Mamo	18	[2]1928	F	2 or 3	20.7	21.5	6		6	
Al	9	[2]1928	M	2 or 3	24.8	33.5	6		7	
Soda	12	[2]1927	F	2	24.4	25.2	7		7	
Bentia	16	[2]1926	F	2	26.9	27.9	8		8	
Cuba	46	March 24, 1926	F	2	29.6	32.4	7	7½	8	
May	32	[2]1925	F	2	30.8	33.0	9		9	
Bokar	5	[2]1925	M	4	36.3	48.2	9		10	
Lia	56	[2]1924	F	1	31.6	34.6	10		11	
Wendy	4	[2]1923	F	1	33.6	36.3	12		12½	
Mimi	44	[2]1923	F	1	45.6	47.1	11		11	
Josie	30	[2]1922	F	2	37.7	41.1	13		13	
Pati	42	[2]1920	F	3	44.3	46.0	15		15	

[1] The least hair is indicated by 1, the best coat of hair by 4.
[2] Estimated date of birth.

Rosy, born at Orange Park, is the daughter of Dita (mother) and Jack. During the first 8 months she grew well, became plump and heavily muscled, but from then on she seemed to be less well nourished and at 11 months was separated from her mother. At that time she was greatly undernourished and for some time after drank milk poorly.

Dick, the son of Josie and Bill, was born at Orange Park. His development, which had been considered normal during the first months of his life, seemed to reach a standstill at the age of one year, at which time he was separated from his mother. Realimentation was not entirely complete when Dick was first used in a metabolism experiment some three weeks later. At this time he was drinking only small amounts of milk and eating limited quantities of solid food.

Bob, the son of Wendy and Bill, was born at Orange Park. During the first ten months of his life he was scrawny, but as he learned to take food other than his mother's milk he began to fill out. At 13 months of age he was separated from his mother and three weeks later was used for the first time in a respiration experiment.

Helene, one of twins born to Mona and Pan at Orange Park, developed slowly for 2 months after birth but thereafter for 4 months gained rapidly. At 7 months of age she began to take small amounts of solid food but depended largely on her mother's milk supply. At about one year of age she was separated from her mother, and by the time she was first used in a metabolism experiment about three weeks later she was drinking milk and eating solid food well.

Tom, the other of the twins born to Mona and Pan, like his sister gained rather slowly for two or three months after which time he began to fill out and take food other than his mother's milk. When he was a little over a year old, he was separated from his mother. Three weeks later, when he was first used in a metabolism experiment, he was considered well nourished.

Ben, the son of Pati and Jack, was born in Orange Park. He was considered relatively large for his age. When he was separated from his mother at one year of age, he was much undernourished. When first used in a metabolism experiment, he was definitely in poor condition. However, he gained rapidly following separation and within a few weeks was much improved.

Gamma, the daughter of Nana and Bill, was also born in Orange Park. She had an uneventful infancy and was well nourished except just before separation from her mother 10 months after birth. Soon after she was again well nourished.

Beta, the daughter of Fifi and Jack, was born in Orange Park. She was small and weak at birth but became firm and well rounded, although still of small size. She was separated from her mother fourteen months after birth. At this time she was not in good physical condition but within four weeks began to show improvement, which was gradual. She is now (January 1936) a well nourished, active, and apparently healthy animal.

Mamo was captured by natives January 24, 1930, in Dinguiraye (Cercle de Dabola), French Guinea, and presented to Yale University by the Pasteur Institute of Kindia. She arrived in Orange Park on June 19, 1930. During the first part of July 1935 there was a suggestion of sexual swelling, at which time Mamo's estimated age was seven years.

Al was captured by natives May 15, 1930, in Labé, French Guinea, and presented to Yale University by the Pasteur Institute. He arrived in Orange Park June 19, 1930. On February 28, 1934, after Al had been mated with Bentia, large numbers of active spermatozoa were found. It is believed that Al was sexually mature at this time, but he had not attained his maximum physical development.

Soda was captured by natives on March 10, 1930, in Nerebili (Cercle de Kindia), French Guinea, and was presented to Yale University by the Pasteur Institute of Kindia.[2] She arrived at Orange Park on June 19, 1930. During the spring of 1935 a slight swelling of the sexual skin was first noticed.

Bentia was captured by natives February 22, 1930, in Baring (Cercle de Kindia), French Guinea, and presented to Yale University by the Pasteur Institute of Kindia. She arrived in Orange Park June 19, 1930. On March 28, 1931, there was a possible slight swelling of genitalia and by May 17, 1933, the swelling was fairly regularly established. On August 31, 1934, bleeding occurred which was identified as menstruation, although slight traces of blood had been observed as early as July 31, 1934.

Cuba was born March 24, 1926, in Havana, Cuba, the daughter of Mona and Jim. For two years following birth she was caged with her mother, Mona. Cuba, the gift of Mr. Pierre S. Abreu to Yale University, arrived in Orange Park May 14, 1931. In December 1932 there was a slight puberty swelling and in April 1933 there was pronounced and irregular sexual skin swelling. On July 10, 1933, when she was 7 yrs. 4 mo. old, a slight menstrual bleeding was first observed. On

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[2] Wilbert, the director of this Institute, in 1929 stressed the usefulness of the chimpanzee for scientific observations.

August 9 (± 5 days), 1934, she became pregnant and on April 11, 1935, she gave birth to the male infant Peter.

May was obtained from the Rockefeller Institute for Medical Research and arrived in Orange Park November 10, 1930. She was not sexually mature at this time and not until May 5, 1932, did she exhibit her first sexual skin swelling. On June 11, 1933, menstruation was first observed.

Bokar was captured by natives March 9, 1930, in Sokili (Cercle de Pita), French Guinea, and presented to Yale University by the Pasteur Institute of Kindia. He arrived in Orange Park on June 19, 1930. On May 4, 1931, he was shipped to New Haven to remain there and to be used in experimental procedures until his return to Florida on May 22, 1933. Motile spermatozoa were noted on November 12, 1932.

Lia is a gift of Mr. Pierre S. Abreu to Yale University. She arrived at Orange Park from Havana on July 6, 1932. Little is known of her previous history except that she first showed signs of sexual skin swelling in May 1931. She menstruated for the first time in November 1932 and became pregnant in August 1933. This pregnancy was terminated on November 13, 1933, with an abortion. When first obtained, Lia was in poor condition but since has improved gradually.

Wendy is one of two chimpanzees purchased from an officer of a ship plying between New York and West Africa. This officer stated that Wendy was purchased by him in the Cameroons. Her history since purchase and up to 1929 has been reported by Bingham (1929). In the spring of 1930 Wendy was transferred to Orange Park from New Haven. The first observed menstrual bleeding occurred on June 23, 1931. On June 27, 1933, she gave birth to a male infant, Bob, who was separated from her on July 25, 1934, at a little over a year of age.

Mimi, a gift of Mr. Abreu to Yale University, reached Orange Park from Havana on May 13, 1931. Her previous history is not known. Genital swelling first appeared on May 12, 1932, and menstruation on July 18, 1932. It is interesting and possibly important that Mimi has shown homosexual tendencies when considered in connection with the fact that she has always been regarded as a large, lank animal in whom sexual maturity appeared rather late. In spite of repeated exposure to vigorous males Mimi has never become pregnant.

Josie, who was formerly an exhibition animal in the private zoo of Mr. George F. Getz of Holland, Michigan, was purchased and sent to Orange Park October 8, 1930. Her keeper stated that two weeks

before being shipped to Orange Park Josie had had a light menstrual flow for the first time. Upon arrival at the station she had a sexual skin swelling. She became pregnant possibly in December 1931 but aborted on June 10, 1932. She again became pregnant and on July 15, 1933, she delivered a full term, healthy male infant, Dick. In January and February 1934 Josie suffered an otitis and paratotitis of the right side, but recovered completely after spontaneous rupture of the ear and the gland. On July 25, 1934, she was separated from her infant.

Pati is another of the animals given to Yale University by Mr. Abreu. While in Havana she gave birth to a healthy female infant, Gua, on November 15, 1930, and was separated from her infant on June 26, 1931, but in the meantime she was transferred to Orange Park on May 13, 1931. It is thought Pati again became pregnant about June 4, 1932, but this pregnancy terminated in abortion on July 16, 1932. She became pregnant about September 10, 1932, and this time gave birth to a male infant, Ben, on May 14, 1933, whom she nursed until separation on May 10, 1934. Although Pati has been troubled with a cough which appears periodically, she has not lost weight but has actually gained weight at Orange Park. She was prone to colds during the early part of her stay in Orange Park, but at present she seems no more susceptible than any other animal. She appears rather listless but dominates her cage mates and at times is vicious in her association with man.

These chimpanzees probably represent many different races and some, especially those born at Orange Park, a cross of races. The group includes chimpanzees ranging in age from two months to probably fifteen years and in body weight from 3 to almost 50 kg. Because of the extreme destructiveness of the adult males, only one (Bokar) could be studied. He had been used in the metabolism chamber before he attained his present weight. That Bokar (who, in the last series of experiments on him, weighed close to 50 kg.) could be used in the metabolism cage is due in part to the fact that when he was more than a year younger and when he weighed only 37 kg. he had been thoroughly accustomed to the cage and the experiment. A factor accounting for his docility in the metabolism chamber is the experience he had encountered not long before in various psychological experiments performed with him in New Haven. These animals were given as nearly as possible ideal conditions for living and were in excellent physical condition at the time of our observations on them, as evidenced by the fact that they were breeding well and normally. In fact, the breeding was so excessive that it was necessary to limit it.

With the exception of May on December 6, 1933, and January 20, 1934, and Lia on November 9, 1933, none of the chimpanzees was pregnant at the time the metabolism measurements were made. No chimpanzee was used which showed symptoms of a cold or other recognizable disease, except that there were usually intestinal parasites, principally Balantidium coli, present. During December 1933 an epidemic of severe colds appeared. All experimental work was suspended during this period. Since the chimpanzees were all living in the same environment, receiving for the most part the same quality and amount of food, having the same number of hours of sleep each day, and leading the same life day in day out, our observations can be considered to have been made on a normal and homogeneous group of animals. Furthermore, the measurements were not confined to one, two, or three animals but included twenty-two individuals, with which a total of 212 respiration experiments were made. The results obtained, therefore, give considerable information regarding the metabolism of the chimpanzee, although there are lacunae in the data still to be filled in. (See page 321.)

Techniques employed

Respiration apparatus

General principle.—Of the various methods of studying the respiratory exchange the one best adapted for work where gas analysis can be employed is the open-circuit method, which is based upon the simple principle of placing the animal inside an hermetically sealed chamber of adequate size, ventilating this at a suitable rate with uncontaminated outdoor air, metering the air passed through the chamber, obtaining an aliquot sample of the air leaving the chamber, and analyzing this sample for its carbon-dioxide and oxygen content. The chamber should not be disproportionately large. On the other hand, it should be of sufficient size to give the animal moderate comfort. This means that since chimpanzees of varying sizes were studied, two sizes of chambers were used. To aid in simplicity, everything was reduced to the simplest terms in that the chamber for the large animals was an air-tight, galvanized sheet-iron shell dropping over a suitable cage and dipping into a water seal, to insure tight closure. For the smaller chimpanzees a water seal at the top of the chamber was preferred. Uncontaminated outdoor air was sucked through the chamber by blowers and next passed through bottles of calcium chloride, where its water vapor was removed. (See figure 1.) It was then metered through a dry gas meter of the ordinary household, 3-light

type. To insure accuracy in the functioning of the meter, two of these inexpensive meters were used in tandem. These were read at the beginning and the end of each period of measurement. If both were functioning accurately, the ratio between the difference in the initial and final readings on the first meter and the difference in the readings on the second meter during the same period of time should remain the same from period to period, and from day to day. Before the air coming from the chamber entered the meter, air samples were withdrawn for subsequent analysis on the Carpenter (1933) gas-

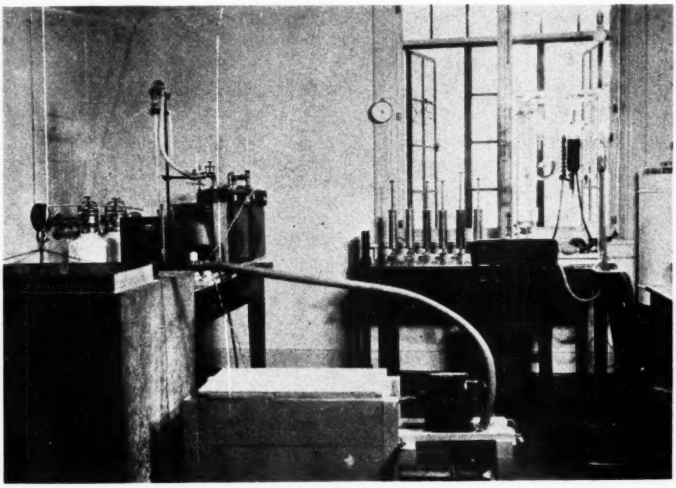

FIGURE 1.—Respiration apparatus for studying the metabolism of the chimpanzee.

At the left is the respiration chamber with galvanized iron cover (suspended on cord and pulley from ceiling) lowered in place over the animal's cage (shown in figure 2). On the table at the right of the chamber are bottles of calcium chloride, a "Fox bag" for collection of an aliquot sample of the out-coming chamber air, two dry gas meters, and a kymograph for recording the activity. On the table by the window are the sampling pumps and a Carpenter gas-analysis apparatus. In the immediate foreground, center, is a blower which in warm weather circulates the chamber air through a metal box immersed in ice water and over an automobile water heater through which ice water circulates.

analysis apparatus. Suitable measurements were made of the temperature of the respiration chamber and of the meters, but as the meters were supplied with dry air, no correction for tension of aqueous vapor was necessary in the calculations. The ventilation was accomplished by a simple rotary air impeller. The rate of flow of air through the system was ascertained either from the rate of rotation of the meter dial or by having in the line a simple flow meter or rotamesser.

Aliquoting and sampling device.—The principle of obtaining an aliquot sample of air leaving the respiration chamber is a simple one devised by Mr. E. L. Fox, late of the Nutrition Laboratory staff. During the experimental period a proportional part of the air from the main air pipe is allowed to pass through a very small opening in a metal disk into a rubber bag (basketball bladder). This disk is inserted in a short length of brass tubing, leading from the main air pipe to the rubber bag. The respiration apparatus is ventilated at such a rate that the carbon-dioxide content of the air in the chamber and that leaving the chamber is maintained at approximately 1 per cent, as this is the optimum carbon-dioxide percentage when analyses are to be made with the Carpenter gas-analysis apparatus (the most essential part of the entire system). To prevent diffusion of carbon dioxide through the rubber bag while the sample of chamber air is being collected, provision is made to have the air leaving the gas meters and having the same composition as the sample blow over the outside of the bag, which is hanging inside a small box. Thus the sample of air inside the bag has essentially the same composition as the air outside the bag, and the sample does not lose or gain carbon dioxide. The details of this Fox bag device have already been described (Carpenter and Fox, 1931; Benedict, 1936).

Activity recording device.—To aid in interpreting the results of the experiments, in so far as the possibility of physical activity vitiating the values is concerned, graphic records were obtained of the degree of muscular repose or the degree of activity of the chimpanzee while inside the respiration chamber. This is done in the case of the adult animal by using a cage which can be securely fastened in position on the chamber base but which has a ¼-inch aluminum plate, hinged at one end and resting on coil springs at the other, for a floor. The entire chamber for the small animals rests upon a platform hinged at one end and resting on coil springs of appropriate size at the other end. A rubber bulb is used under the spring end of the aluminum plate or the platform, and this rubber bulb is connected with a tambour. Thus the slightest change in the body position of the animal is imme-

diately reflected by the variations in pressure on the bulb, and these variations in pressure are in turn graphically recorded by a tambour (connected with the bulb or pneumograph), whose pointer writes the record of the animal's activity on smoked paper on a kymograph drum. (See figure 2.) Proof of the sensitivity of the activity recording device was had in each case by connecting the kymograph and tambour with the moveable platform before the chamber cover was put in place. This permitted observing what effect the animal's movements had on the activity record while the animal was still visible.

Respiration chamber for small chimpanzees.—The chamber that was used for chimpanzees up to 10-kg. in weight consisted of a tinned copper box, 46 cm. long, 35 cm. wide, and 25.5 cm. high (inside dimensions), having a capacity of 41 liters. Around the top of the box was a trough containing water, into which the cover of the box fitted, making a water seal. Air entered the chamber from one end and was deflected by a baffle plate upward and away from the animal. Air left the chamber at the other end. In the cover of the chamber was inserted a thermometer, the bulb of which was 6 cm. below the cover.

Cages for confining adult chimpanzees.—As the small chimpanzees are easily handled, no provision was made for caging other than placing them in the chamber. The situation is quite different, however, with the adults, who are extremely powerful and destructive. One of the first practical problems, therefore, in the handling of these larger chimpanzees was the construction of a cage which would be light enough to be carried and yet be sufficiently strong to withstand the destructiveness of the animals. The first cage built for this purpose was made of oak and fastened together with bolts and screws. Heavy wire netting was fastened inside the oak frame and braces in such a manner as to prevent the animal's being able to secure a grip on any part of the cage. The bottom of the cage was an aluminum plate, ¼ inch or 6 mm. thick. This oak cage was heavy and by virtue of its construction allowed insufficient room for the larger animals. Its inside measurements were 59 cm. (length) by 41 cm. (width) by 63 cm. (height). Its outside measurements were 66 cm. by 58 cm. by 71 cm. It weighed about 59 kg. In addition to the oak cage, a steel cage was constructed of steel window grills welded together. (See figure 2.) The floor construction of this steel cage was essentially the same as that of the wooden cage. The total weight of this cage was only 43 kg. Its outside measurements were 65 cm. (length) by 47 cm. (width) by 74 cm. (height) and its inside measurements 61 cm. by 44 cm. by 66 cm. A sliding door in the front of each cage permitted opening and closing of the cage.

Base and cover of chamber for adult chimpanzees.—The base of the chamber was durably constructed and bolted to the floor of the laboratory. It was provided with angle-iron anchorages into which the bolts of the chimpanzee's cage fitted. The air intake and outlet, as well as the connections to the rubber bulb of the activity recording

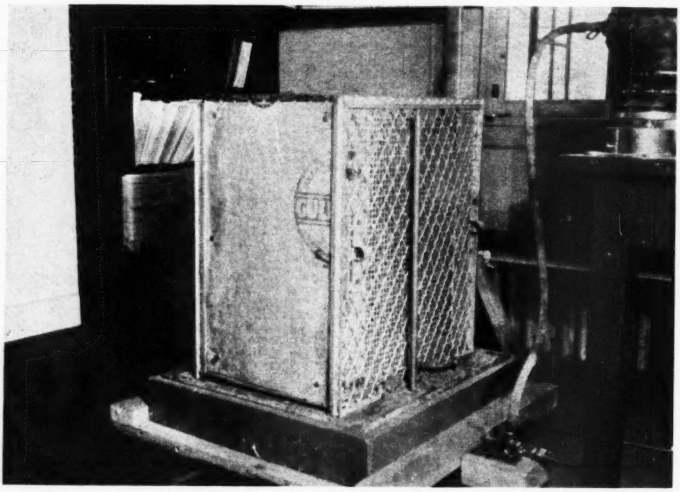

FIGURE 2.—Steel cage for large chimpanzees, fastened to base of respiration chamber.

Around the base to which the cage is attached is a narrow trough used as a water seal when the galvanized iron cover (see figure 1) is in place. At the upper right-hand side of the photograph is seen the kymograph upon which is recorded the chimpanzee's activity.

device were provided in this base. A trough of water around the outside edges of the base provided a water seal when the chamber cover was lowered into place. The cover was constructed of galvanized sheet-iron and measured 72 cm. by 63 cm. by 81 cm. When the cover was in place over the base (as shown in figure 1), its height from the floor was 74 cm. The capacity of the chamber was approximately 336 liters. However, when the chamber is in use, the residual volume is considerably less, for one must make allowances for the volume occupied by both the animal and the cage.

Control of temperature of respiration chamber.—The temperature of the chamber for small chimpanzees was regulated either by an electric glow heater with the heat directed on the outside of the chamber, or (when it was desired to lower the temperature) by a wet muslin cloth placed on the chamber, over which a current of air from a fan was directed. In a few experiments on days when the temperature of the room was exceptionally high, a small cake of ice was placed on top of the chamber. A tray was soldered on the top of the chamber used for the large animals. Here ice was placed, making it possible to maintain a satisfactory temperature. Additional cooling of the larger chamber was secured by means of a blower, which re-circulated the air in the chamber through a metal box containing an automobile water heater. This box was immersed in ice water and ice water was circulated also through the heater. (See figure 1.)

Gas analysis.—The chamber air samples were stored, dry, in sampling pumps (Lee, 1933) for 10 to 14 hours and were analyzed on the Carpenter gas-analysis apparatus.

Control of accuracy of functioning of respiration chamber.—The entire apparatus was thoroughly tested and checked by means of alcohol and carbon-dioxide recovery tests in Boston before being sent to Orange Park. Immediately upon assembly at Orange Park and at frequent intervals thereafter alcohol was burned in the chamber and its respiratory quotient determined. In all instances the quotients were close to the theoretical quotient for alcohol. In addition to these precautions to insure accuracy of functioning of the apparatus, samples of outdoor air were analyzed before any analyses of the collected air samples were begun.

Typical calculation of results

The observations made during a typical experimental period and the method of calculating the results to the basis of total heat production per 24 hours are shown in table 2. The gas sample collected in the Fox bag was withdrawn from the bag into sampling pumps. The total sample in the case of the experimental period illustrated in table 2 was the equivalent of seven pumpfuls, and as each pump held 370 c.c., the total volume of the sample was 2.590 liters. This volume was added to the corrected meter reading to obtain the true total volume of air passing from the respiration chamber during the period of measurement. Since outdoor air was introduced into the chamber, the percentage of carbon dioxide in the air sample as determined by the Carpenter gas-analysis apparatus was reduced by 0.030 to correct for the percentage of carbon dioxide in outdoor air.

TABLE 2

TYPICAL CALCULATION OF RESULTS

Animal Experiment 198 Period 3 March 27, 1935
Start, 8.40 p.m. Duration, 20.00 min.
Wendy, female, 35.8 kg. Removed from food 7.30 a.m., March 27, 1935

Meter readings

	Meter A	Meter B
End	4726.2 l.	6901.0 l.
Start	4334.7 l.	6510.2 l.
Difference	391.5 l.	390.8 l.

Meter ratio, 391.5 ÷ 390.8 = 1.002

Temperature and pressure readings

	Chamber	Meter	Room	Rotamesser	Manometer	Aneroid Barometer
	°C.	°C.	°C.		mm.	mm.
Start	27.0	27.1	27.8	25.5	11	760.0
End	26.3	27.1	27.8	24.5	11	760.0

Gas analysis

Volume of gas sample: 2.590 liters

$$\frac{CO_2 \text{ increment } (\%)}{O_2 \text{ deficit } (\%)} = \frac{0.622}{0.829} = 0.75 \text{ R.Q.}$$

Calculations

Volume of air passing through meter A	391.5 liters
Times meter factor	× 0.996
Corrected metered volume	389.9 liters
Plus volume of gas sample	+ 2.6 liters
Total ventilation	392.5 liters
Times factor for reduction to 0° C. (dry), 760 mm.[1]	× 0.910
Reduced ventilation	357.2 liters
Divided by time	÷ 20.0 minutes
Reduced ventilation rate per minute	17.86 liters
Times O_2 deficit	× 0.829 p.ct.
O_2 per minute	0.1481 liter
Times caloric value of O_2 at R.Q. of 0.75[2]	× 4.739 cal.
Times 1440 minutes	× 1440
Total heat production per 24 hours	1010.7 cal.

[1] Factor for average meter temperature (27.1° C.) and barometric pressure (760 mm.) according to table 10 in Carpenter's tables (1924a).

[2] Carpenter, 1924b.

Conditions under which the basal metabolism measurements were made

No problem was of any greater interest to us than the general survey of the basal metabolism of the chimpanzee. Man has been studied extensively, and although great variations in metabolism exist both with males and with females, particularly during the age of growth, nevertheless a general average figure for the basal metabolism of males is one calorie per kilogram of body weight per hour. With the average man weighing 60 kg. this would amount to 1,440 calories per day. Numerous observations on women and children have also been made and the effects of growth, variations in size (particularly in adiposity), and age are reasonably well known with man. A similar and as extensive a study with the chimpanzee is ultimately desirable. The effects of all these factors could not be determined during the progress of our investigation on the chimpanzee, although the attempt was made to meet as nearly as possible this ideal situation. Since the number of chimpanzees available is limited when compared with the number of human subjects available, our first function was to establish suitable conditions for basal metabolism measurements.

Muscular repose.—What are the conditions under which the metabolism of the chimpanzee may be expected to be basal? According to previous experience, primarily with man, the first essential is muscular repose. With the chimpanzee, therefore, every effort was made to rule out activity. To this end the animals were studied at the time of day when they were accustomed to be quiet, that is, during the evening, usually at the time when they normally went to sleep and when the external sounds around them were reduced to a minimum.[3] The chimpanzee, given a bag to lie on while inside the respiration chamber, usually curled up and apparently was sound asleep during most of the experiment. Rarely was an evening's experiment lost because the animal was too active. Occasionally a twenty-minute or a half-hour period of activity would appear between two quiet periods, but as a rule the physical repose of these chimpanzees is in striking contrast to that of the macaques, animals with which the Nutrition Laboratory has had long experience. With these latter it ultimately became necessary to use "nembutal" to insure measure-

[3] With the macaques (unpublished experiments) the Nutrition Laboratory has found it imperative to make the basal metabolism measurements at night, in order to secure muscular repose. Night experiments have likewise been found to be essential with pigeons and doves (Benedict and Riddle, 1929).

ments under comparable conditions of repose. Although the chimpanzees were studied in complete darkness and could not be seen during the experiment, the graphic tracings on the kymograph drum indicated the degree of repose or activity. In the final analysis of the data these kymograph records were assessed without reference to the results of the metabolism measurements, in fact, before the calculation of the results. Periods of complete or nearly complete repose were graded as I; those of some but not excessive activity as II; and those of considerable activity as III. All periods with activity III were discarded in the final summarization of the data.

Sleep.—A factor that plays a great role in the metabolism of humans but which has thus far not been adequately considered with other animals is sleep. In the cage, the chimpanzee when awake is curious and inquisitive, picking at the bag and examining all parts of the cage. If the graphic record of activity showed little or no movement there is every reason to believe that the chimpanzee was not only lying quietly but in all probability was asleep. Since the animals were as a rule unusually quiet, it is believed that they were sound asleep in most of the experiments. There is, however, no certain proof of this. With man the basal metabolism has been found to be, in general, about ten per cent lower while asleep than while awake. In any comparisons of our basal metabolism measurements on the chimpanzees with basal metabolism measurements on animals of other species it must be borne in mind that the chimpanzees, in all probability, were studied when asleep.

Post-absorptive state.—The second prerequisite for basal metabolism measurements was that the chimpanzee should be in the post-absorptive condition. This was controlled by withdrawing food a number of hours prior to the experiment. Again based on experience with man, twelve hours were deemed essential for this purpose. At 7.30 a.m. the animal was given its breakfast, consisting of chimcracker and fruit. Thereafter for the rest of the day food was denied. To insure that no food was given throughout the day previous to the experiment (which took place in the evening), the chimpanzee's name and the date on which it was to be used in an experiment were posted in a conspicuous place in the animals' diet kitchen. Occasionally a chimpanzee was used in a psychological test on the morning of the same day when a metabolism experiment was to be made. In such instances the small amount of food given to it as a reward during the psychological observations was fed not later than 10 a.m., and the metabolism measurements were started later than usual in the evening so that the animal's fasting period would be sufficiently long.

Normal body temperature.—Another condition essential in any study of basal metabolism is that the body temperature should be normal. Unfortunately, body temperature measurements were not made in our research. It is perhaps regrettable that the rectal temperatures of the smaller chimpanzees were not recorded, for observations on them would have presented no serious problem. In the case of the larger chimpanzees such records could be made only with great difficulty. The normal life of these animals and the relatively complete absence of infectious diseases lead, however, to the belief that there were no instances of abnormal body temperature during the metabolism study, although direct proof of this is not available.

Environmental temperature.—Another condition essential for the measurement of basal metabolism is that the external temperature should not stimulate the heat production of the animal. In other words, the measurements should be made in the zone of thermic neutrality, and it is important to establish this zone fairly accurately. For this reason, although the majority of the observations were made at chamber temperatures between 25° and 29° C., a few were made at temperatures as low as 17° C. Thus it was possible to determine how great the deviation from 28° C., the temperature of thermic neutrality for many animals, might be before an increase in metabolism would take place as a result of the stimulus of the temperature.

With the exceptions of Bokar and Cuba who spent the entire winter of 1933–34 in unheated quarters, the animals were in a sense able to choose an environmental temperature to their liking. During the cold season the animal usually prefers the warm winter sun to the heated living room where the temperature is maintained at 20° C., except when there is an unusually cold spell of about 0° C. During the warm months the animals can take advantage of shade, which is provided for in part of the cage. Thus, although no attempt was made to keep the animal in a stable and fairly warm environmental temperature for 24 hours previous to the experiment, the animal could choose a temperature that was at least suitable to his comfort.

Records were kept of the temperature, taken not in the cage actually but in a location with approximately the same protection as the cage would supply. These records give the temperatures of the environment only when the animal is outside. As has been stated before, the animal would be inside in a temperature of 20° C. on extremely cold days.

Bokar and Cuba during the winter of 1933–34 lived outside in a large enclosure. They were provided with a covered bed box for

protection against rain and wind, but no heat was supplied to this protection. On one or two occasions when the temperature was 0° C. or lower, Bokar and Cuba were given quarters in the heated building during the night.

Precautions against noise during the experiment.—Ordinarily the chimpanzee is very alert to its surroundings and responds to any strange noise. Consequently it was necessary to take precautions against any disconcerting noise in the experimental room during the experiment. Such precautions consisted in entering the room carefully and only to read meters, thermometers, etc., and to collect the air sample at the end of the period; in wearing rubber soled shoes when walking in the room; and in avoiding in every possible way noise of any kind. It was found by experience that loose boards in the floor that would creak when stepped upon would occasionally disturb an animal. This was especially true with May. One of us actually went into the chamber and had the chamber cover lowered. Under these circumstances it was found that footsteps in the room could be heard very well in the chamber, possibly due to direct transmission to the base of the chamber which is bolted to the floor, but that noises outside of the room or building could be heard scarcely or not at all. When the experiments were begun, it was thought that the gas analysis could be done at the time the animal was in the chamber, but this was soon abandoned with considerable improvement in the activity record. There were striking exceptions, however. Noise that might provoke considerable activity on one night might prove entirely inadequate to stimulate the same animal on another night.

Apparently there was not much adaptation to the situation after that which occurred in the first hour or so of experience in the chamber. It was found that a preliminary period of training was unnecessary, and that there was no tendency for the metabolism to be higher on the first night than on later trials. Nevertheless in experiments extending over a period of two months, during which two of the chimpanzees were studied every other night, as many precautions against noise had to be taken on the last evening as on the first.

Procedure during the respiration experiment.—The routine followed with the adults was as follows: Shortly before 5 p.m. the adult chimpanzee was transferred from its living quarters to the metabolism cage, and the cage was placed in position on the base of the respiration chamber in the laboratory. Usually the chamber cover was lowered between 7 and 8 p.m. The temperature of the chamber was then ad-

justed, and ten minutes after the cover was lowered the ventilation of the chamber was started. If the chimpanzee became quiet immediately and remained quiet, the aliquot sampling of the outcoming chamber air was begun 45 minutes later. Occasionally a wait of over two hours was necessary before sampling could begin. Rarely was an evening unproductive of periods of comparative quiet, however, even when the chimpanzee was used for the first time. When the experiment was completed, usually at about 11 p.m., the animal and the cage were weighed together. The animal was then transferred to its living quarters and fed, and the cage alone was weighed. The routine with the small chimpanzees differed little from that with the adults, except that the animal was carried in the arms to and from the metabolism chamber without being confined in a cage.

Discussion of results

The results of the basal metabolism measurements made during periods of muscular repose and twelve hours after food are recorded in tables 3 to 9 for the various chimpanzees studied. In four instances (November 16, 1933, and March 14, 1934, with Bokar; January 30, 1934, with Lia; and March 13, 1934, with Mimi) the values for a given date are based upon only one 20-minute period of observation. In all other instances they represent averages based on from two to six, usually four, 20-minute periods. In a few of the experiments the activity was of grade II (see page 278), but in the majority of cases it was of grade I.

Tabular presentation of data

For purposes of considering subsequently the metabolic effects of such factors as age, sex, and size, and particularly for comparison of the metabolism of the chimpanzee with that of other species of animals of different sizes, it is necessary to have some method of expressing the metabolism whereby the differences in body weight will be at least in part equalized. For these reasons the metabolism values given in tables 3 to 9 are reported not only on the basis of the metabolism of the animal as a whole, that is, the total heat production per 24 hours, but on the basis of the heat production per kilogram of body weight and per two-thirds power of the body weight. One of the earliest methods of comparing the metabolism of different animals was in terms of the heat production per unit of body weight. This method has a defect, however, in that it assumes that the heat-producing power of the body substance is the same per kilogram of weight

TABLE 3

Basal Metabolism of Young Male Chimpanzees

Chimpanzee and date	Body weight	Chamber temperature	Respiratory quotient	Heat production per 24 hours		
				Total	Per kg.	Per 10 $w^{2/3}$
1934	kg.	°C.		cal.	cal.	cal.
Peter						
June 14[1]	2.94	26.5	0.75	226	76.8	1100
July 24[1]	3.85	26.8	.76	273	70.8	1108
Don						
Apr. 11[1]	4.80	25.4	.76	255	53.1	894
Apr. 19[1]	5.08	25.9	[2].73	290	57.0	978
Dick						
Aug. 15	5.30	27.5	.77	289	54.5	951
Aug. 29	5.42	27.0	.74	299	55.2	971
Sept. 11	5.86	28.9	.81	333	56.8	1024
Bob						
Aug. 14	4.44	28.8	.80	295	66.5	1093
Aug. 28	4.92	27.1	.77	284	57.8	983
Sept. 12	5.39	28.0	.81	310	57.5	1009
Tom						
Aug. 6	6.84	27.2	.82	330	48.3	917
Aug. 22	7.58	27.1	.81	380	50.1	985
Sept. 5	7.64	26.9	.77	353	46.2	910
Ben[3]						
May 17	4.79	26.1	.76	210	43.8	738
May 21	4.75	27.1	.81	203	42.8	719
May 30	5.18	26.5	.81	229	44.2	766
June 6	5.49	26.3	.78	275	46.0	834
June 13	5.74	26.8	.77	282	49.2	879
Aug. 9	6.98	27.4	.80	311	44.6	852
Aug. 20	7.36	27.2	.80	333	45.2	880
Sept. 4	7.76	27.2	.78	358	46.2	915

[1] 1935

[2] 21 hours without food instead of the usual 12 hours.

[3] Not included in table 10, page 310, as undernourished at start.

irrespective of whether the bodies of the animals compared are made up of the same proportions of bone, muscular tissue, water, and fat. Nevertheless this method has had long usage and is at times distinctly helpful. The procedure of referring the metabolism to the surface area has also had long usage, as a result of the stress laid upon it by Rubner. This method rests upon the general thesis that the heat lost to the environment is proportional to the area of the body, and that

TABLE 4

BASAL METABOLISM OF ADULT MALE CHIMPANZEES

Chimpanzee and date	Body weight	Chamber temperature	Respiratory quotient	Heat production per 24 hours		
				Total	Per kg.	Per 10 $w^{2/3}$
	kg.	°C.		cal.	cal.	cal.
Al[1]						
June 19, 1934	25.0	27.4	[2]0.76	858	34.3	1004
June 27, 1934	24.8	26.4	[2].73	919	37.1	1082
July 6, 1934	25.3	27.5	[2].73	946	37.4	1098
May 13, 1935	33.0	25.9	.81	1033	31.3	1004
May 16, 1935	33.3	27.4	.82	1110	33.4	1073
May 29, 1935	32.9	26.3	.78	1099	33.4	1070
May 31, 1935	33.5	25.1	.76	1138	34.0	1095
June 4, 1935	33.3	26.7	.76	1047	31.5	1012
Bokar[3]						
Nov. 16, 1933	37.1	28.4	.76	1091	29.4	982
Nov. 23, 1933	36.6	26.6	.76	1025	28.0	930
Nov. 28, 1933	36.3	27.8	.79	961	26.5	877
Jan. 15, 1934	37.0	19.5	.78	1043	28.2	941
Jan. 22, 1934	37.3	22.2	.75	1108	29.7	993
Feb. 6, 1934	36.8	19.4	.81	1100	29.9	995
Feb. 13, 1934	37.2	19.5	.77	1102	29.6	989
Feb. 20, 1934	37.0	19.4	.77	1093	29.5	985
Feb. 27, 1934	37.1	20.0	.75	1084	29.2	976
Mar. 14, 1934	38.3	26.6	.77	1111	29.0	978
June 20, 1935	48.2	26.4	.74	1315	27.3	993
June 25, 1935	47.9	28.4	.74	1138	23.8	863

[1] Considered adult on May 13, 1935, and thereafter.

[2] 28 hours without food instead of the usual 12 hours.

[3] Living outdoors all the time, as was Cuba. No access to heated quarters, as in case of other chimpanzees.

TABLE 5

BASAL METABOLISM OF YOUNG FEMALE CHIMPANZEES

Chimpanzee and date	Body weight	Chamber temperature	Respiratory quotient	Heat production per 24 hours		
				Total	Per kg.	Per 10 $w^{2/3}$
1934	kg.	°C.		cal.	cal.	cal.
Rosy						
Apr. 9[1]	4.35	26.6	[2]0.76	263	60.5	989
Apr. 18[1]	4.74	25.4	[2].76	260	54.8	921
Helene						
Aug. 7	5.34	28.4	.77	326	61.0	1065
Aug. 21	5.96	27.1	.81	341	57.2	1036
Sept. 6	6.00	27.6	.75	306	51.1	928
Gamma						
Mar. 7	6.69	26.7	.75	379	56.7	1068
May 8	7.14	27.6	.76	392	54.9	1056
May 18	7.03	26.0	.77	385	54.7	1049
May 24	7.62	25.8	.76	391	51.3	1010
May 29	7.34	26.2	.74	407	55.5	1077
June 5	7.32	26.9	.77	382	52.2	1012
June 12	7.38	26.0	.75	342	46.4	903
June 13[1]	12.0	27.2	.76	450	37.5	858
Beta						
Mar. 9	8.94	25.3	.75	392	43.8	910
May 7	9.86	27.4	[2].71	505	51.2	1098
May 15	10.08	26.5	.76	489	48.5	1047
May 22	10.21	26.5	.75	482	47.2	1022
May 28	9.80	25.5	.74	483	49.3	1055
June 4	9.84	27.1	.75	470	47.7	1024
May 1[1]	14.2	26.2	.73	513	36.1	873

[1] 1935.

[2] 21 to 28 hours without food instead of the usual 12 hours.

in order to keep the temperature of the body constant the heat production must equal the heat lost. Consequently the heat production is proportional to the surface area. It is unnecessary to go into the details of the development of this most interesting hypothesis, but for decades this has dominated the thought of many physiologists. In

the practical use of this method of expressing the metabolism, it is essential to have some suitable means of determining the surface area of the animals actually being studied. This can be done by sacrificing the animal, removing the skin and measuring it with a planimeter. Obviously this is not practical in most cases, and recourse was quickly had to various formulas based upon some measurable factor, notably, in the early stages, the weight. Vierordt (Meeh, 1879) early proposed that the surface area was proportional to the two-thirds power of the weight (in grams) multiplied by a constant, K. This constant was supposed to vary considerably, depending upon the body configuration of the different animals. A recent analysis, however, has shown that the constant remains singularly uniform for all animals and close to 10 (Benedict, 1934). In the case of the macaque Lee and Fox (1933) have shown by planimetering of the skins removed from several different animals that the value of K is equal, on the average, to 11.7. With two chimpanzees weighing 14.1 and 24.5 kg. Bruhn (1934),

TABLE 6

BASAL METABOLISM OF ADOLESCENT FEMALE CHIMPANZEES

Chimpanzee and date	Body weight	Chamber temperature	Respiratory quotient[1]	Heat production per 24 hours		
				Total	Per kg.	Per 10 $w^{2/3}$
1934	kg.	°C.		cal.	cal.	cal.
Mamo						
June 15	20.7	27.7	0.73	773	37.4	1026
July 2	21.0	27.9	.75	780	37.2	1025
July 11	21.5	27.4	.74	734	34.1	949
Soda						
June 22	24.5	27.6	.76	871	35.6	1032
June 29	24.4	28.1	.74	841	34.5	1000
July 10	25.2	27.4	.74	905	36.0	1053
July 13	24.8	28.9	.77	841	33.9	990
Bentia						
June 18	26.9	27.2	.75	821	30.5	914
June 26	27.2	28.5	.73	889	32.7	983
July 3	27.0	26.0	.76	863	32.0	959
July 12	27.9	27.3	.73	854	30.6	928

[1] 27 to 28 hours without food instead of the usual 12 hours.

TABLE 7

BASAL METABOLISM OF ADULT FEMALE CHIMPANZEES

Chimpanzee and date	Body weight	Chamber temperature	Respiratory quotient	Heat production per 24 hours		
				Total	Per kg.	Per 10 $w^{2/3}$
Cuba[1]	kg.	°C.		cal.	cal.	cal.
[2]Nov. 8, 1933	31.7	23.2	0.77	1018	32.1	1016
Nov. 17, 1933	31.7	27.4	.79	1001	31.6	999
[3]Nov. 22, 1933	30.1	26.4	.75	985	32.7	1018
Nov. 27, 1933	29.6	28.3	.74	974	32.9	1018
[4]Dec. 12, 1933	31.5	27.0	.79	1102	35.0	1105
[5]Jan. 5, 1934	31.4	27.8	.73	1155	36.8	1161
[6]Jan. 10, 1934	32.0	26.2	.83	1189	37.2	1180
[2]Jan. 17, 1934	31.1	19.6	.74	1065	34.3	1078
[2]Jan. 26, 1934	32.4	28.0	.81	1017	31.4	1001
[7]Feb. 2, 1934	31.0	19.7	.80	1046	33.8	1060
[6]Feb. 8, 1934	30.7	27.7	.81	1023	33.3	1043
[8]Feb. 16, 1934	31.0	27.5	.77	1042	33.6	1055
[7]Mar. 16, 1934	32.2	24.2	.78	1090	33.9	1077
May						
[7]Nov. 7, 1933	32.7	25.1	[9].73	1074	32.8	1050
[3]Nov. 14, 1933	32.7	27.5	.78	1004	30.7	981
Nov. 20, 1933	32.7	27.4	.79	1058	32.4	1034
[6]Nov. 24, 1933	30.8	28.3	[9].71	1120	36.3	1139
[10]Dec. 6, 1933	31.8	27.7	.74	1251	39.3	1246
[7]Jan. 11, 1934	32.5	26.8	.76	1094	33.7	1075
[11]Jan. 20, 1934	31.6	27.6	.77	1002	31.7	1002
[8]Jan. 31, 1934	31.3	21.0	.74	989	31.6	996
[12]Feb. 5, 1934	32.0	28.0	.80	1361	42.6	1351
[2]Feb. 12, 1934	32.4	28.7	.75	1069	33.0	1052
[7]Feb. 19, 1934	33.0	28.0	.76	1239	37.6	1204
Lia						
[13]Nov. 9, 1933	32.4	25.9	.77	1309	40.4	1288
Nov. 21, 1933	31.7	26.7	.73	1009	31.9	1008
Dec. 1, 1933	32.8	26.6	.74	1081	33.0	1055
[6]Dec. 7, 1933	32.5	26.5	.81	1131	34.9	1112
[2]Jan. 4, 1934	32.4	26.8	.78	998	30.8	983
[2]Jan. 9, 1934	32.4	25.1	[14].87	1155	35.7	1139
[7]Jan. 16, 1934	31.6	19.2	.76	1294	41.0	1294
[8]Jan. 24, 1934	31.9	28.0	.76	1151	36.1	1144
[8]Jan. 30, 1934	32.3	18.8	.80	1256	39.0	1240
[2]Feb. 9, 1934	33.6	28.0	.77	1087	32.4	1044

TABLE 7—(*Cont.*)

Chimpanzee and date	Body weight	Chamber temperature	Respiratory quotient	Heat production per 24 hours		
				Total	Per kg.	Per 10 $w^{2/3}$
Lia (cont.)	kg.	°C.		cal.	cal.	cal.
[2]Feb. 15, 1934	33.4	26.5	.79	991	29.7	955
[2]Feb. 23, 1934	33.9	27.3	.75	1007	29.7	962
[2]Mar. 2, 1934	33.5	26.3	.79	1002	29.9	964
[7]Mar. 8, 1934	34.6	28.1	.81	939	27.1	884
[3]Mar. 15, 1934	33.0	20.3	.76	1021	31.0	992
Mar. 30, 1935	33.0	26.0	[9].76	1121	34.0	1090
[2]Apr. 29, 1935	33.9	26.0	.79	1051	31.0	1004
[3]May 2, 1935	33.5	25.4	.73	979	29.3	943
[15]May 15, 1935	33.6	27.7	.79	851	25.3	817
[3]June 3, 1935	33.7	27.5	.75	967	28.7	928
Mimi						
[3]Jan. 12, 1934	47.1	27.0	.74	1318	28.0	1011
[7]Jan. 18, 1934	46.7	27.8	.75	1504	32.2	1160
[2]Jan. 25, 1934	47.1	28.0	.76	1288	27.3	988
[7]Feb. 1, 1934	45.6	27.5	.76	1504	33.0	1179
[3]Feb. 7, 1934	45.7	28.3	.78	1367	29.9	1070
[2]Feb. 21, 1934	46.0	28.5	.75	1342	29.2	1046
[2]Feb. 28, 1934	46.3	21.0	.76	1573	34.0	1220
[2]Mar. 13, 1934	46.6	24.8	.76	1727	37.1	1334
Pati						
Mar. 15, 1935	44.9	24.8	[9].77	1165	26.0	922
Mar. 20, 1935	46.0	26.2	.78	1202	26.1	936
[3]Apr. 6, 1935	44.7	27.9	.76	1141	25.5	905
[2]Apr. 15, 1935	44.6	25.7	.78	1207	27.1	960
[3]May 6, 1935	44.3	27.1	.77	1102	24.9	880
May 21, 1935	44.9	26.1	.74	1107	24.7	876

[1] Living outdoors all the time, as was Bokar; no access to heated quarters, as in case of other chimpanzees.
[2] Maximal genital swelling.
[3] Menstruating.
[4] Maximal genital swelling. Symptoms of a cold; nasal discharge and cough.
[5] Coughed; restless; passed foul liquid feces while in chamber.
[6] Increasing genital swelling.
[7] Decreasing genital swelling.
[8] Permanent residuum.
[9] 21 to 28 hours without food instead of the usual 12 hours.
[10] Decreasing genital swelling; possibly pregnant. (See page 307.)
[11] Menstruating or having miscarriage. (See page 307).
[12] Permanent residuum; active.
[13] Pregnant. (See page 307).
[14] Possibly obtained cracker from animal in next cage.
[15] Fifteen days after beginning of last bleeding.

TABLE 8

Basal Metabolism of Adult Female Chimpanzee Wendy

Date	Body weight	Chamber temperature	Respiratory quotient	Heat production per 24 hours		
				Total	Per kg.	Per 10 $w^{2/3}$
1934–35	kg.	°C.		cal.	cal.	cal.
[1]Oct. 10	35.9	28.3	[2]0.94	887	24.7	815
[1]Oct. 12	34.9	26.6	.76	1052	30.1	985
[3]Oct. 20	34.9	27.9	.78	1063	30.5	996
[3]Oct. 22	35.3	26.3	.84	892	25.3	829
[3]Oct. 24	35.4	26.7	.86	999	28.2	927
[3]Oct. 31	34.3	26.3	.79	906	26.4	858
[3]Nov. 2	34.9	26.9	.77	892	25.6	835
[3]Nov. 4	34.6	26.5	.79	902	26.1	850
[4]Nov. 6	34.9	25.8	.76	1011	29.0	947
[4]Nov. 8	35.6	26.2	.80	1068	30.0	987
[4]Nov. 10	35.7	26.7	.81	1027	28.8	947
[1]Nov. 12	35.3	26.8	.78	1049	29.7	975
[1]Nov. 14	35.9	26.9	.77	1073	29.9	986
[1]Nov. 16	35.5	26.2	.80	1088	30.6	1007
[1]Nov. 18	35.6	25.9	.76	1036	29.1	958
[5]Nov. 20	35.0	26.4	.75	1005	28.7	939
[3]Nov. 22	35.0	26.7	.80	1119	32.0	1046
[3]Nov. 24	35.0	25.9	.75	1005	28.7	939
[3]Nov. 26	34.4	26.4	.76	1081	31.4	1022
[3]Nov. 28	34.8	26.9	.77	1061	30.5	995
[6]Nov. 30	34.8	27.4	.77	927	26.6	870
[6]Dec. 2	35.2	26.1	.82	1008	28.6	938
[3]Dec. 4	35.2	26.7	.77	921	26.2	858
[3]Dec. 6	34.6	26.4	.78	980	28.3	922
[3]Dec. 8	35.1	26.2	.85	1012	28.8	944
[3]Dec. 10	35.4	28.4	.83	1047	29.6	971
[4]Dec. 12	35.3	27.4	.80	1035	29.3	962
[4]Dec. 14	35.6	26.7	.83	1063	29.9	983
[4]Dec. 16	35.6	26.5	.76	1060	29.8	979
[1]Dec. 18	35.9	28.7	.74	1021	28.4	939
[1]Dec. 20	35.7	26.3	.82	978	27.4	903
[1]Dec. 22	36.3	26.4	[2].93	1072	29.6	979
[3]Dec. 28	35.5	27.3	.74	1037	29.2	960
[3]Dec. 30	35.3	26.3	.85	972	27.6	903
[1]Feb. 26	35.1	25.2	[7].73	1052	30.0	981
[1]Feb. 27	35.0	22.7	.76	1008	28.8	942

TABLE 8—(*Cont.*)

Date	Body weight	Chamber temperature	Respiratory quotient	Heat production per 24 hours		
				Total	Per kg.	Per 10 $w^{2/3}$
1934–35	kg.	°C.		cal.	cal.	cal.
[5]Feb. 28	34.6	17.8	[7].74	1243	35.9	1171
[1]Mar. 27	35.8	26.7	.75	999	27.9	920
[6]Apr. 12	34.3	25.3	.76	1165	34.0	1104
[1]Apr. 23	35.8	26.3	.75	946	26.4	871
[6]May 14	34.9	27.4	.81	897	25.7	840
[1]May 23	34.4	25.8	.74	963	28.0	910
[6]June 12	33.6	26.5	.76	937	27.9	900

[1] Maximal genital swelling. (See lowest curve in fig. 3, page 298.)
[2] May have obtained food.
[3] Permanent residuum.
[4] Increasing genital swelling.
[5] Decreasing genital swelling.
[6] Menstruating.
[7] 21 to 28 hours without food instead of the usual 12 hours.

TABLE 9

BASAL METABOLISM OF ADULT FEMALE CHIMPANZEE JOSIE

Date	Body weight	Chamber temperature	Respiratory quotient	Heat production per 24 hours		
				Total	Per kg.	Per 10 $w^{2/3}$
1934–35	kg.	°C.		cal.	cal.	cal.
[1]Oct. 11	38.8	28.6	0.73	1088	28.0	949
[2]Oct. 19	39.1	27.0	.78	1090	27.9	946
[2]Oct. 21	39.3	27.4	.79	1052	26.8	910
[3]Oct. 23	39.5	27.7	.78	1050	26.6	905
[3]Oct. 25	41.1	26.6	.79	1028	25.1	863
[3]Oct. 27	37.7	27.2	.79	1097	29.1	977
[4]Oct. 29	38.8	27.5	.76	1064	27.5	929
[1]Nov. 1	38.4	28.2	.80	1129	29.4	992
[1]Nov. 3	38.8	28.3	.80	1118	28.8	975
[5]Nov. 7	39.0	26.3	.81	1164	29.8	1012
[1]Nov. 9	39.3	26.9	.82	1124	28.6	973
[1]Nov. 11	38.5	25.5	.82	1098	28.5	963
[1]Nov. 13	38.5	26.6	.78	1117	29.0	979
[1]Nov. 15	38.4	25.1	.80	1100	28.7	967

TABLE 9—(*Cont.*)

Date	Body weight	Chamber temperature	Respiratory quotient	Heat production per 24 hours		
				Total	Per kg.	Per 10 $w^{2/3}$
1934–35	kg.	°C.		cal.	cal.	cal.
[1]Nov. 17	39.1	26.5	.79	1100	28.2	955
[2]Nov. 19	38.8	26.3	.77	1118	28.8	976
[2]Nov. 21	39.2	26.5	.77	1099	28.0	952
[2]Nov. 23	39.0	27.2	.77	1140	29.2	991
[3]Nov. 25	39.0	25.4	.78	1101	28.2	957
[3]Nov. 27	39.0	26.4	.78	1133	29.1	985
[3]Nov. 29	40.0	26.2	.77	1012	25.3	864
[3]Dec. 1	39.4	26.1	.78	1114	28.3	962
[3]Dec. 3	40.2	27.6	.80	1050	26.1	894
[3]Dec. 5	39.8	25.9	.78	1067	26.8	915
[4]Dec. 7	39.8	27.1	.81	1056	26.5	906
[1]Dec. 9	39.3	28.7	.82	1109	28.2	960
[1]Dec. 11	39.1	26.3	.82	1078	27.6	935
[6]Dec. 13	39.8	26.5	.81	1125	28.3	965
[6]Dec. 15	40.4	27.0	.84	1163	28.8	988
[6]Dec. 17	39.5	27.2	.80	1138	28.8	981
[1]Dec. 19	39.0	25.8	.81	1076	27.6	936
[1]Dec. 21	40.0	26.0	.83	1014	25.3	867
[1]Dec. 27	39.8	26.0	.78	1072	26.9	919
[2]Dec. 29	38.7	26.6	.80	1035	26.8	905
[2]Dec. 31	39.9	26.2	.82	1067	26.8	914
[2]Jan 2	39.5	25.0	.79	977	24.7	842
[2]Jan 4	40.2	26.3	.80	988	24.6	841
[3]Jan. 6	39.5	26.3	.82	1010	25.6	871
[3]Jan. 8	40.1	27.3	.82	1039	25.9	886

[1] Permanent residuum. (See fig. 4, page 299.)
[2] Increasing genital swelling.
[3] Maximal genital swelling.
[4] Decreasing genital swelling.
[5] Menstruating.
[6] Slight genital swelling.

employing the procedure of Du Bois and Du Bois (1915), found values of 11.0 and 10.5, respectively.

Because the general survey of the body surface constants for all the animals, with configurations varying as greatly as from that of the frog to that of the horse, has shown that the constant is close to 10 and because it is desired ultimately to compare the metabolism of the

chimpanzee with that of other animals (commonly expressed per square meter of body surface), the values obtained for the total heat production of our chimpanzees have been divided by the two-thirds powers of their weights and multiplied by the factor 10. For convenience in discussing the heat values expressed on this basis we shall refer to them in the pages and tables that follow as the heat production or the calories "per 10 $w^{2/3}$". As pointed out in the general survey mentioned above (Benedict, 1934), the magnitude of the inherent error in the constant 10 is much less than that in the basal metabolism measurements that are to be compared.

Thus we have three methods for comparison of the metabolism data, the total heat production, the heat production per unit of weight, and that per 10 $w^{2/3}$. These three methods of expressing the results are believed to be sufficient for the study of the several factors that might influence the chimpanzee's metabolism, and no other method of computation is justifiable with our present series of chimpanzee measurements, comprehensive though they are.

The respiratory quotient as an index of the post-absorptive state

The common index of the post-absorptive state employed in most experiments with humans and with animals in general has been the respiratory quotient, that is, the relationship between the carbon-dioxide production and the oxygen consumption. With herbivorous animals (the chimpanzee must be considered as essentially a Herbivore) one would expect a fairly high respiratory quotient at the end of a meal. With ruminants and most large domestic animals whose food intake consists primarily of carbohydrates the quotient is practically at unity when they are on feed. When the food material in the alimentary tract has been absorbed, however, the animal ultimately reaches a condition where its body heat must be derived almost wholly from the combustion of fat. In this condition the respiratory quotient is more nearly 0.70.

With man immediately after food ingestion the gaseous metabolism is high as a result of the digestive processes, but it soon decreases rapidly until it reaches a lower, fairly constant level from which it only slowly decreases thereafter. This period of essential constancy in the metabolic level, when the active period of digestion has ceased, occurs with man at about twelve hours after food ingestion, and at this time the respiratory quotient is not far from 0.82. With the chimpanzees a study was not made of the course of the respiratory

quotient and the decrease in heat production following food intake. The majority of the metabolism measurements were made 12 hours after food. A few were made about 24 hours after food. Examination of the respiratory quotients of the several chimpanzees listed in tables 3 to 9 shows that values of 0.71 to 0.73 were obtained when the animal had been without food for about 24 hours (May on November 7 and November 24, 1933, and Beta on May 7, 1934) and that values ranging from 0.73 to 0.86 and averaging 0.78 were obtained 12 hours after food. It may, therefore, be concluded that the chimpanzees were in the post-absorptive state when the metabolism measurements were made. That this condition is reached in only twelve hours is perhaps explained by the nature of the chimpanzee's food (which is concentrated and contains but a small amount of fiber) and by the rate of passage of the food through the intestinal tract, a rate which in spite of the herbivorous diet may be relatively rapid.

Factors affecting basal metabolism, as shown by the detailed data for individual chimpanzees

Emotional excitement and influence of training

Because of the general nervousness of the chimpanzee and its tendency to excitability, especially as the result of group stimulation, one would expect that emotional excitement might have an effect upon its basal metabolism. With man it has been found that the metabolism is noticeably increased by emotional strain (Benedict, 1935). According to the Nutrition Laboratory's experience with macaques the first measurement on any one of these animals is apt to show a very high metabolism. As it is necessary to use a net to capture the macaque and the animal engages in considerable strife in the attempt to avoid being put into the metabolism cage, there are two factors contributing to its high metabolism, the after-effect of muscular work and the after-effect of the emotional upset. The animals at Orange Park have been generally conditioned to experimental conditions for years and, therefore, no trouble was experienced in transferring the animal from its living quarters to the metabolism cage. The younger chimpanzees could all be handled by the observers and readily came to the observer for study without the excitement and alarm of being "caught" in a net. The adult chimpanzees as well as the younger ones soon adapted themselves to the restrictions of the metabolism cage or chamber, and no trouble was experienced in enticing them into the cage. Hence the after-effect of previous muscular effort did not play a role. But it might be expected that the

factor of emotional tension might be present, especially during the first experiment when the chimpanzee might be stimulated by the novelty of being placed in a strange and confining environment. It was quickly found, however, that practically no training was required for these animals to adjust themselves to the conditions of the experiment, for usually the metabolism in the first experiment was as low as that in the later experiments and sometimes even lower. Hence it can be concluded that the respiration chamber and the procedures of technique in the experiments were in no sense disturbing to the emotional make-up of these chimpanzees and that no long period of training is necessary. One might expect, however, that a recently captured wild chimpanzee would behave very differently, indeed, more like the macaques in the Baltimore colony.

Environmental temperature

In the many respiration experiments that have been made on numerous animals, one factor has been demonstrated to have an especially marked effect upon the metabolism, namely, the environmental temperature. In his early classic experiments on the metabolism of dogs, Rubner selected as a convenient environmental temperature that of the laboratory, at that time 16° C. All his measurements on dogs were made at this temperature. In a subsequent comparison of the metabolism of dogs with the metabolism of other animals care was not taken to have the same environmental temperature in all cases. Subsequently it has been shown that most animals, notably dogs, have a profound reaction to the environmental temperature in that the metabolism is high at the lower temperatures and becomes lower as the temperature increases until at about 28° C. the minimum metabolism is reached. This is not true of all animals. Some, such as the rat, show a reaction to temperature when there is the slightest deviation from 28° C. Others, like the goose and the sheep which are well protected animals, do not show any effect of temperature until it reaches approximately 12°, 10° C., or below. Even the short-haired animals, such as the steer and the horse, do not experience any increase in their metabolism until the temperature of their surroundings is considerably below 20° C. The temperature range over which an animal can be studied without having its metabolism affected by the temperature has been termed by Lefèvre the "zone of thermic neutrality." It was believed that this zone should be established with the chimpanzee although, based upon previous experience, it was assumed at the start that this animal's metabolism would reflect

the ordinary finding with other animals and that if the measurements were made between 25° and 28° C. they would be obtained well within the zone of thermic neutrality.

The role played by the environmental temperature at the time of measurement, however, is a transitory one when compared with that played by the temperature of the environment in which the animal is living permanently. Hence in any analysis of the results obtained at given experimental temperatures one should take into consideration whether the animal's living conditions have necessitated an adjustment of its entire organism, possibly by an increase in metabolism, to combat a low environmental temperature. *A priori* one would expect to find that the metabolism of animals accustomed to living at a low temperature would be higher even when measured in the zone of thermic neutrality than the metabolism of animals of the same species accustomed to living at a warmer temperature, and that the zone of thermic neutrality would be wider. The width of this zone might also be affected considerably by the condition of the animal's fur. Consequently during the study of the effect of environmental temperature (made chiefly to make certain that temperatures of 25° to 28° C. were not outside the zone of thermic neutrality) observations were included on two chimpanzees, Bokar and Cuba, that had been exposed for a long time to an outdoor life and considerable temperature fluctuations and hence had undergone what may certainly be termed a "hardening process." Of these two animals, Bokar had a fine coat of hair and Cuba not such a good coat. (See table 1.) Because the degree of hair protection would be expected to play a considerable role in helping to resist the cold environment, measurements were also made on one chimpanzee that was defectively haired, being almost without any hair covering (Wendy), and on another (Lia) that was only moderately well haired. These two latter animals were not made to live constantly outdoors but had access to the warmer inside living quarters, when they desired. With each of these four chimpanzees a few metabolism measurements were made between 17° and 24° C., as well as at the higher temperatures of 25° to 29° C.

With Bokar there was a singularly uniform series of measurements at 19° to 22° C., the values ranging only from 941 to 995 calories per 10 $w^{2/3}$. (See table 4.) At 25° to 28° C. the range is wider, from 863 to 993 calories. Two values under 900 calories occur with temperatures of 28° C., but at this same temperature a value as high as 982 calories also occurs. The conclusions are that the lower temperature had no appreciable effect upon this animal's metabolism and that in his case

the zone of thermic neutrality is in all probability 10° C. in width, *i.e.*, from 19° to 28° C. With Cuba (see table 7) there was again no effect of temperatures as low as 19.6° C., and the zone of thermic neutrality is as wide in her case as with Bokar. Apparently the effect of a temperature of 20° C. was not pronounced with Lia (see table 7) but at 19° C. the metabolism was 27 per cent above the average at 20° to 28° C. With Wendy (see table 8) all but two of the experiments were made at temperatures between 25° and 28° C. These show an average heat production per 10 $w^{2/3}$ of 939 calories. In one experiment at 23° the heat production was 942 calories and in one at 18° it was 1,171 calories. At the lowest temperature the metabolism was 25 per cent above the average (939 calories) at 23° to 28° C. As Wendy was almost hairless, it is surprising that her reaction to the low temperature was not proportionately much greater than was the reaction of Lia, who was somewhat better haired. Inasmuch as with the three chimpanzees, Bokar, Lia, and Wendy, no obvious metabolic effect of environmental temperatures as low as 20° to 22° C. was noted, it can be inferred that *the chimpanzee's zone of thermic neutrality may be as wide as from 20° to 29° C., irrespective of the amount of hair protection. With chimpanzees accustomed to living outdoors, temperatures from 17° to 19° C. likewise have no effect, but with chimpanzees not inured to the cold, temperatures below 20° C. will cause a decided increase in metabolism.*

Further experiments at high and low environmental temperatures are desirable with chimpanzees of greatly differing body weights as well as varying amounts of hair, to determine whether the subcutaneous fat supplements the lack of hair. It is probable that it does not. There is also the problem as to whether the activity of the thyroid gland is stimulated by the low temperatures, which might explain why the two chimpanzees accustomed to living outdoors showed no metabolic effect of temperatures below 20° C. Against this explanation, however, is the fact that the basal metabolism of these two chimpanzees at thermic neutrality was no higher than that of the two chimpanzees not inured to cold. In fact the average metabolic level expressed as the heat production per 10 $w^{2/3}$ was essentially the same with all four animals.

A natural explanation of the absence of reaction to cold might be based upon the old conception of the relationship between surface area and heat loss, namely, that the chimpanzees had done everything they could to reduce the area for heat loss by assuming their characteristic pose in a cold environment. This pose can best be described

by calling it a squat, Indian fashion, often one foot holding the other, the back flexed ventrally, and the arms drawn across the abdomen and thorax. In this position the chimpanzee is simulating the shape of a ball and hence certainly decreasing the surface area of the skin exposed to the cold environment. On the other hand, the chimpanzees are rarely observed shivering at temperatures of 20° C. in the absence of rain or wind, even when the sun is obscured. This reduction in the surface area of the skin exposed to the cold environment may be, in a certain sense, comparable to the reduction in surface area effected by a group of animals in huddling, but it has been repeatedly demonstrated by experiments on other animals that huddling *per se* does not reduce the metabolism (Benedict and Ritzman, 1931; Benedict and Fox, 1933, 1934). The thought that the chimpanzees may have partially covered themselves with the bag given them to sleep on while inside the respiration chamber also suggests another possible means of their reducing their skin area. As heat production is a central rather than a peripheral effect, the local loss at any one point may be varied within very wide limits without affecting in any way the total heat production.

Because man is ordinarily either clothed or covered with bedding, his zone of thermic neutrality when thus artificially protected is very wide. Even the Australian savage with his entire absence of clothing can withstand great differences in environmental temperature without significant alterations in metabolism (Hicks, Moore, and Eldridge, 1934).

Variability in the basal metabolism of the chimpanzee

It is known from experience with man and other animals that the basal metabolism is not constant during the period of growth, but the problem arises as to what variations are to be expected in the basal metabolism of the adult animal from day to day, from week to week, or from month to month. In other words, how labile is the basal metabolism of the adult chimpanzee? Is its metabolism so constant over a period of weeks or months that it would be justifiable to measure it once at the beginning or end of an experimental series and use this measurement as a baseline to study the effect of some subtle, superimposed factor, or is it so variable that it must be determined each day before the measurement of the effect of the superimposed factor? With Wendy, the basal metabolism was measured at approximately 2-day intervals from October 10 to December 30, 1934, and at irregular intervals thereafter until June 12, 1935. The data are, therefore,

available for an analysis of the variability in metabolism studied almost every other day for a period of two and one-half months. The results of those metabolism observations made *within the zone of thermic neutrality* are illustrated graphically by the three uppermost curves in figure 3. Although the maximum variation in body weight amounted to only eight per cent during the period of experimentation, the changes in weight have likewise been indicated by a curve near the bottom of the chart. As menstruation is likewise a factor to be taken into consideration in any study of the metabolism of the adult female chimpanzee, the menstrual and intermenstrual periods are indicated by the lowest curve at the bottom of the chart. Discussion of this curve and its relation to the metabolism curves will be deferred until our analysis of the menstrual factor *per se*. (See page 302.)

The extreme variability in Wendy's total heat production at thermic neutrality[4] between October and June of the following year was from 887 calories on October 10 to 1,165 calories on April 12, that is, an increase of 31 per cent. Although the minimum value on October 10 is confirmed by four other low points near the start of the curve, the maximum value on April 12 is considerably higher than any point on the rest of the curve. The fact that Wendy was menstruating on this day may have played a role. The effect of this particular factor will be considered subsequently. (See page 302.) During the first month the variability is particularly great, and the question may properly be raised as to whether one would be justified in using an average of *all* the measurements on Wendy to represent her basal metabolism. However, if the data for each 2-week interval were averaged throughout the entire series, one would find that these 2-week averages would, for the most part, be close to the general average of 1,008 total calories. The last four measurements in April, May, and June are at a definitely lower level, averaging 936 calories. The curves for the heat production per kilogram of body weight and per 10 $w^{2/3}$ have much the same form as the curve for the total heat production, which is to be expected as there was so little variability in the body weight.

With Josie, observations were made likewise at essentially 2-day intervals over a period extending from October 11, 1934, to January 8, 1935. The results are shown graphically in figure 4, the order and the style of the curves being the same as in figure 3. In Josie's case also the maximum variability in body weight was less than 10 per cent,

[4] Not including the metabolism measurement on February 28 at 17.8° C.

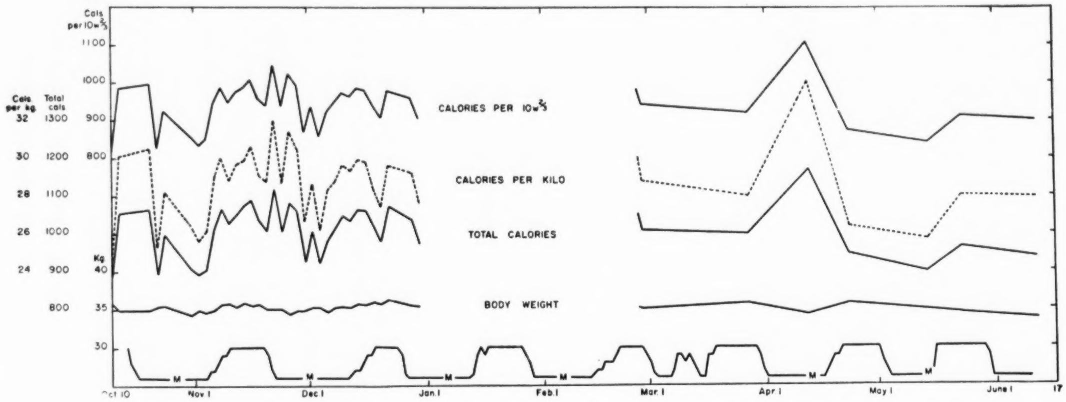

FIGURE 3. Variability in the basal metabolism of the female chimpanzee Wendy, studied at thermic neutrality over an 8-month period.

At the base of the chart is a curve indicating the menstrual dates (M) and the degree of sexual skin swelling on the intermenstrual days. Next in order is the body weight curve and above this the curves for total heat production per 24 hours (full line), heat production per kilogram of body weight (short-dash line), and heat production per 10 $w^{2/3}$ (full line.)

and hence the trends of the three heat curves are much the same. There are several low points on these curves, most of them occurring in the latter half of the series. Between October 25 and October 27 there was a considerable change in Josie's weight without a corresponding change in the same direction in the total heat production. On three previous dates, October 19, 21, and 23, her weight had ranged only from 39.1 to 39.5 kg. On October 25 it increased to 41.1

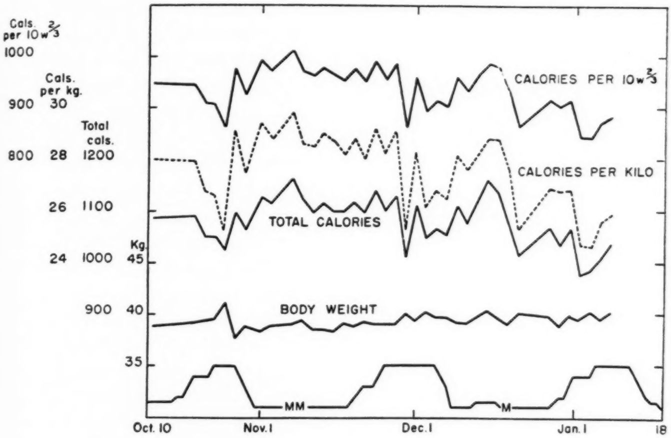

FIGURE 4. Variability in the basal metabolism of the female chimpanzee Josie, studied at thermic neutrality over a 3-month period.

At the base of the chart is a curve indicating the menstrual dates (M) and the degree of sexual skin swelling on the intermenstrual days. Next in order is the body weight curve and above this the curves for total heat production per 24 hours (full line), heat production per kilogram of body weight (short-dash line), and heat production per 10 $w^{2/3}$ (full line).

kg., and her total heat production decreased slightly from a level of 1,050 to 1,028 calories. On October 27 her weight decreased to 37.7 kg. and her total heat production increased to 1,097 calories. In other words, in two days there was an 8 per cent *decrease* in body weight and a 7 per cent *increase* in total heat production. The maximum variability in the total heat production is from 977 calories to 1,164 calories, a range of 19 per cent or considerably less than was noted with Wendy. The general average value for the total heat

production is 1,082 calories and the averages for the 2-week intervals vary from this, at the most, only by 5 per cent.

The selection of an average value to represent the metabolism of Wendy and similarly of Josie is of great importance for subsequent comparisons of the several chimpanzees, to study the relations of age, growth, and sex to metabolism. One immediately asks what values could be used for these animals other than the general averages. In the case of Wendy the average 24-hour heat production per 10 $w^{2/3}$ is 939 calories and in the case of Josie, 936 calories. From figures 3 and 4 it is seen that a low value of about 850 calories for the heat production referred to 10 $w^{2/3}$ was obtained at times with both chimpanzees. Were there only one such point, little weight could be placed upon it, but as there are several on widely separated days and with both animals, the real existence of this low metabolic level seems confirmed. The question, therefore, arises as to why the average of these low values should not be used to represent the basal metabolism instead of the average based upon the entire series of measurements. From the very definition of the words "basal metabolism" one could make the assumption that it is impossible to find a metabolism *below* basal. Hence it would seem that one should use the minimum measurements as basal. With Wendy the average of the values under 900 calories is 847 calories or 10 per cent below her general average heat production of 939 calories. With Josie the average of the values under 900 calories is 866 calories or 7 per cent below her general average. Why do these low points in the curves exist? In metabolism studies limited to a period of days or at the most a month or so there is only one physiological factor known actually to depress the metabolism, and that is sleep. But under the experimental conditions the chimpanzees were all supposedly asleep. Their deportment and the graphic records of activity suggest that they were asleep. Unfortunately we could not actually see them. The only logical explanation for the low metabolism values is that the chimpanzees were in an unusually deep sleep during these particular measurements. This explanation is most unsatisfactory. It may be that at the time of these low measurements the metabolism was in a state of flux, comparable to the condition noted in experiments with large ruminants at the University of New Hampshire (Benedict and Ritzman, 1935), although such a state is not believed to exist in the case of well-conditioned humans (Benedict, 1935).

With the other chimpanzees the experimental series were not so extensive. Analysis of the data for Wendy and Josie proves, however,

that the average value of all the measurements may justifiably be used to represent their basal metabolism in general comparisons and that although a three-month series of observations on the other chimpanzees would have been ideal, nevertheless an average of any series of measurements extending over two weeks or more should give a reasonably accurate basal value. However, figures 3 and 4 show strikingly that it is unwise not to recognize that the metabolism of any given chimpanzee tends to be variable, in fact, much more variable than is the case with humans. *Hence in the study of the effect of any superimposed factor, especially when the effect is a small and subtle one, it is not permissible to use an average, pre-determined value to represent the basal metabolism. One must measure the basal metabolism immediately before studying the effect of the superimposed factor. The average basal value is of importance only in general comparisons of one animal's metabolism with that of another animal of the same species.*

Effect of season

With man it has been much debated whether there is an effect of season *per se*. Observations by Palmer, Means, and Gamble (1914) indicate a lower heat production in the summer than in the winter, although the body weight of their subject remained the same. The experiments of Gessler (1925) and Griffith *et al.* (1927, 1929) likewise indicate that the energy expenditure is lowest in summer. In a study of students at Wellesley College, however, the metabolism was found to be at a low level during the winter and to rise to a higher level during the spring and summer (Gustafson and Benedict, 1928). It was hoped that with this group of chimpanzees some information might be obtained as to whether a change in season affects the metabolism or not. Season as such involves so many different factors that it is difficult to analyze their separate effects. Even in the latitude of Orange Park (ca. 30°) change in season means a considerable change in environmental temperature, humidity, and hours of sunlight, although by no means so great as in the higher latitudes. In the case of captive animals fed by man the variations in the nature of the foodstuffs according to the season of the year are not so great as the variations in these other factors, although without doubt some foods are more plentifully fed when in season than when not. One would expect the most pronounced effects of change in season to be accounted for by the environmental temperature or the ultra-violet light. Clothing minimizes the effect of light upon the metabolism of humans, and changes in clothing in large part compensate for changes in environmental temperature.

Careful analysis of the observations on the adult chimpanzees, with whom the factor of growth would play no role, and particularly an analysis of the observations on those animals studied over a long period of time show no positive effect of season. The scattered observations on Wendy in May and June (see figure 3) suggest that her metabolism was lower at this time of year than in the fall and winter. This, however, is contrary to the experience with large domestic animals, whose metabolism usually increases in the spring.[5] These animals, however, are put out to pasture in the spring where they have access to fresh green food. The diet of the chimpanzee is subject to no such change. Therefore any observed effect could not be due to a change to a more or less stimulating diet as might possibly be the case with domestic animals.

The menstrual cycle and energy metabolism

Menstruation in women produces a physical effect that may be classified under three heads, (1) extreme discomfort and much pain, (2) a feeling of malaise, depression, and exhaustion, or (3) no discomfort. It would be expected that if menstruation were accompanied by severe pain and discomfort the metabolism would be increased. On the other hand, if menstruation resulted in a feeling of lassitude or exhaustion, the tendency would be toward a lower metabolic rate. It is the common belief that civilization is responsible, for the most part, for woman's discomfort during menstruation. There is no evidence that the chimpanzee experiences pain or discomfort or is exhausted during menstrual bleeding. This animal is more comparable to the woman studied by Benedict and Finn (1928), who experienced no pain. Since it has been shown that in woman regardless of whether or not discomfort or exhaustion is an accompaniment of menstruation, there is variation in the metabolic rate, it was of considerable importance to study the female chimpanzee carefully. The adult female chimpanzee manifests a rhythmic alteration of the genital tract—the sex cycle.[6] During this cycle the animal may be subject to alterations in its temperament and activity (Yerkes and Elder, 1936).

[5] Unpublished experiments made by Professor E. G. Ritzman at the University of New Hampshire.

[6] Descriptions of the sex cycle, sexual skin swelling, length of sex cycle, and menstruation in the chimpanzee have been given by Hartman (1932), Parkes and Zuckerman (1931), Sokolowsky (1923), Tinklepaugh (1933), Yerkes and Elder (1936), Zuckerman (1930, 1931a, 1931b, 1932), and Zuckerman and Parkes (1932).

Josie and Wendy, the two subjects of the investigation on the menstrual cycle, were selected as examples of mature female animals. Each had given birth to and reared infants to the age of one year. They were cage mates and were living under as nearly the same environment as possible. Here the similarity of the animals stops. Wendy had little or no hair, due principally to the fact that she denudes large areas of herself, whereas Josie had a moderately good coat of hair. These two animals were used at approximately two day intervals during two successive menstrual periods. Both animals were in good health and at the beginning of the experiment each had been separated from her infant for about three months. The menstrual cycle was well established at this time.

As it is apparent from observations on humans that the effect of menstruation, if it exists, is a subtle one, a careful analysis was made of the metabolism measurements on Wendy and Josie prior to the plotting of the data in figures 3 and 4, to rule out measurements made during periods of unusual activity (which were rare) and to rule out any days when only a single period of measurement was secured. A value for any one experimental day was not considered unless there were at least two well-agreeing periods for that day. The variability in the metabolism of Wendy and Josie from day to day over a long period of time has already been discussed. (See page 296.) The high and low levels in the curves shown in figures 3 and 4 were interpreted as characteristic of the normal variability in the basal metabolism of the adult female chimpanzee. Our problem now is to compare and, if possible, to correlate these variations in metabolism with the menstrual cycle, with particular reference to the genital swelling. For this purpose, the lowest curve in each chart has been drawn to give a suggestion as to the approximate degree of rapidity of increase and decrease in the size of the genitalia and the duration of the period of bleeding, in this latter instance indicated by the letters MMM. At the beginning of the experimental series the period of sexual swelling of Wendy coincided with the period of menstruation with Josie.

The observations made on the maximum outdoor temperature on the day preceding the night of the experiment and the observations on the relative humidity have not been incorporated in figures 3 and 4. The relative humidity varied during the three months from October 10 to January 10 from 38 to 90 per cent, and the average minimum relative humidity was about 60 per cent. Examination of the protocols for Wendy and Josie shows no correlation between the outdoor maximum temperature or relative humidity and the variations in

heat production. All the metabolism measurements represented in figures 3 and 4 were made at chamber temperatures between 23.0° and 28.7° C., and the majority of them at about 26° C. We have already shown that these temperatures are well within the zone of thermic neutrality for the chimpanzee. Thinking that possibly the chimpanzee would show a temperature reaction similar to that of the rat and some other animals, that is, unless the chimpanzee were kept for some hours before the respiration experiment at a temperature within its zone of thermic neutrality its metabolism would be high, we have examined the room temperature at which the chimpanzees were kept for four hours previous to the experiment. We have found not the slightest indication that a room temperature of 20° C., which was the lowest noted during the four hours preceding the experiment, has any influence on the heat production. This is to be expected since the zone of thermic neutrality for the chimpanzee is very wide, from 20° to 29° C. Various other factors such as activity, excitement, and food, which, on the basis of experience with other animals, are known to influence the heat production were either controlled or ruled out. As pointed out on page 300, difference in depth of sleep might account for some of the variability noted in the metabolism of Wendy and Josie, but as both were supposedly asleep in all experiments it must be assumed that the depth of sleep was not greater at one part of the menstrual period than in another. The only known factor, therefore, that might influence the results obtained on Wendy and Josie (plotted in figures 3 and 4) is the sex cycle.

The heat curves for Wendy plotted in figure 3 show, in general, a low metabolism during bleeding and a higher metabolism in the intermenstrual periods. The average of all the determinations on Wendy from October 10 through December 30, 1934, expressed as the heat production per 10 $w^{2/3}$, is 940 calories. The mean for the two ten-day periods including and following the onset of bleeding (October 31 and November 2 and 4; November 30, December 2, 4, 6, and 8) is 884 calories. The mean for all other dates between October 10 and December 30 is 957 calories. The difference between these two means is of sufficient magnitude to be statistically reliable and a real fact.

Although the chimpanzee is believed not to experience, during menstruation, the malaise and pain felt by women, nevertheless it is more apt to be lethargic and quiet during this period. For this reason one may challenge the apparently low metabolism of Wendy during her period of bleeding. The question may naturally be asked as to whether her feeling of lassitude was so great that she was completely

relaxed during the experiments. If so, the activity records should show that on these menstrual days there was less activity. With a view to discovering whether or not this factor was having an effect, two members of the Nutrition Laboratory staff independently examined *all* the activity records of Wendy and each selected the ten days on which, according to their judgment, the kymograph records indicated the minimum activity. It so happened that eight of the ten days selected by the two individuals were the same, namely, October 22, November 8, 16, 18, 20, and 22, and December 4, 1934, and March 27, 1935. The other two days were October 20, 1934, and May 14, 1935, according to one of the staff members and October 10 and November 2, 1934, according to the other member. On six of these days the metabolism was low (below 1,000 total calories) and on six it was high. This argues against lassitude or lack of activity playing a role in the low values obtained.

The picture shown by the data for Josie, plotted in figure 4, is entirely different from that for Wendy. In Josie's case the metabolism was studied through three consecutive periods of sexual swelling, and in each instance her lowest metabolism is recorded during the period of swelling. The ten days of least activity in Josie's case (judged by one person by examination of the kymograph records alone without reference to the metabolism measurements) were October 11, 12, and 27, November 3, 13, and 19, and December 11, 13, 19, and 27, 1934. On all of these days the higher metabolism values were obtained. The mean of all the determinations on Josie is 936 calories per 10 $w^{2/3}$. The mean for the two ten-day periods counting from the first day of bleeding (November 7, 9, 11, 13, and 15; and December 19, 21, and 27) is 952 calories. The mean for all the other days of observation is 932 calories, or slightly lower. However, if one divides the cycle into 10-day periods and determines the mean of the first, second, and fourth 10-day periods (October 11; November 7, 9, 11, 13, 15; December 19, 21, 27; November 17, 19, 21, 23, 25; December 29, 31; January 2, 4, 6; October 29; November 1, 3; December 7, 9, 11, 13, 15, 17) it will be found to be 943 calories, whereas the mean for the third 10-day period (October 19, 21, 23, 25, 27; November 27, 29; December 1, 3, 5; January 8) will be 919 calories. Thus Josie's lowest metabolism occurred during the period of greatest swelling.

From the results on these two chimpanzees one can not say exactly what the influence of the menstrual cycle is on the heat production. That there is some effect is fairly well shown by the analysis of the curves in figures 3 and 4 for Josie and Wendy, although the effect

comes at different parts of the menstrual cycle in these two cases. This is not irreconcilable with the observations on women. It is generally accepted that the metabolism of women is far more variable than that of men, and it is thought that this variability in part is due to the effect of the menstrual cycle. Not all women, however, show variations that can be correlated with the cycle. With some there is no significant change in metabolism. With others there are peaks and depressions in the metabolic level, but these high and low levels do not occur at the same time of the menstrual cycle in different women. Benedict and Finn (1928) studied an artist's model who was phlegmatic in disposition and never experienced any discomfort during menstruation. She was aware of menstruation only as a result of bleeding. Hence she may be considered to have been physiologically normal. With this woman there was a depression of the metabolic rate on menstrual days, a peak on pre-menstrual days, and another peak on the intermenstrual days. Hitchcock and Wardwell (1929) studied 20 women, of whom 14 showed a lowering of heat production during menstruation, one showed no change, and five an insignificant rise. Ten experienced a decrease of five per cent on the menstrual days. There was a suggestion of an intermenstrual drop on the twelfth to the twenty-third days of the cycle (the first day of the cycle being the first day of menstruation). Griffith (1929) and his colleagues reported a peak in metabolism on the pre-menstrual days and a decrease on menstrual days. Conklin and McClendon (1930) found that nine of the ten women they studied had low metabolic rates immediately following and high rates just preceding menstruation. The instances with women in which there is a depression in metabolism during the menstrual days are comparable to the situation with Wendy and those instances of women showing an intermenstrual decrease are comparable to the situation with Josie.

In addition to the above two experiments, which were planned to study the effect of the sexual cycle, observations were made on five other animals which, although they are not complete for the entire cycle, offer certain comparisons. May had a metabolic rate lower on November 14, when she was menstruating, than her average rate on the other days. Lia, who was studied on three menstrual days, gave low values on these days. Cuba studied on one, Pati on two, and Mimi on two menstrual days showed no change in metabolism from the intermenstrual days.

Metabolism during the period of puberty

The exact time of beginning of ovulation has not been determined in the chimpanzee, but for the monkey it is known that menstruation precedes ovulation by some months. That this is true for the chimpanzee is supported by the fact that no animal has ever become pregnant immediately after the animal first menstruated, but only after a period of eight or more months. If this is true, then both May and Cuba had not yet ovulated when first used in metabolism experiments but possibly started while they were being used. The metabolism for May and Cuba, expressed per 10 $w^{2/3}$, is somewhat higher than for three other adolescent females, Bentia, Soda, and Mamo and for the adult female Pati, but is not far from that of the adult females Mimi and Lia (when 10 years old). Our data give no indication that there is an increased metabolism of puberty for the female chimpanzee.

Metabolism as affected by pregnancy

The metabolism of none of the chimpanzees was studied throughout a period of pregnancy. Only one observation was made when we were sure that the animal was pregnant, namely on Lia on November 9, 1933, but this day was Lia's first experience in the chamber. It has been said that only seldom was the metabolism higher in the first experiment than on subsequent days. An inspection of the data for Lia on November 9 shows that in all periods the activity was of grade II. The figure obtained for the metabolism on this day is not comparable, therefore, with other figures obtained on days when all or nearly all periods were of grade I activity. It is not believed that the metabolism on November 9 shows the effect of pregnancy on metabolism. On November 13 Lia aborted a 40-gram fetus, which was estimated to be three months old. It is barely possible that whatever was responsible for the abortion was operating on November 9, making Lia restless and hence producing a high metabolism.

May was used in an experiment on December 6, 1933, when early pregnancy was suspected. On this date she had some symptoms of a cold. Her metabolism was high. Unfortunately no body temperature records were taken. On January 20, 1934, blood appeared from the vagina, but it is not known whether this was due to delayed menstruation or whether it was an early abortion, since at so early a date no attempt was made to recover the fetus.

Factors affecting basal metabolism as shown by comparison of the average metabolism values for the several chimpanzees studied

From close inspection of the detailed data for the several chimpanzees listed in tables 3 to 9 the conclusion has been drawn that, for purposes of comparing the metabolism of the different chimpanzees, the general average of all the metabolism measurements on each chimpanzee can be used as representing the basal metabolism of that particular animal when there was no marked change in body weight. Secondly, since with two of the chimpanzees periods of measurement of only two or three weeks showed essentially the same average metabolism as the averages for successive 2-week periods during three continuous months of experimentation, it is also concluded that the average of measurements limited to a 2-week period (in spite of low and high values) may be accepted as indicative of the probable average basal metabolism, even though the animal was under observation for less than a month. In the third place, although it may be legitimately contended that the true basal or irreducible minimum is that represented by the low values that occur in a few instances (which are 10 to 15 per cent below the general average), it is assumed at present that the only adequate explanation for these low values is that they represent the effect of profound sleep. As a result of this careful analysis of our data, average values for the total heat production, the heat production per kilogram of body weight, and that per 10 $w^{2/3}$ have been derived for each of the chimpanzees studied. In a few instances when the chimpanzee was studied over a long time and there was an appreciable difference in weight and an increase in age, the problem arises as to whether one general average value should be used. How great a variation in weight and in age may be permitted before the chimpanzee should be considered as a larger and older animal? This problem as to how great the change in body weight or age must be to warrant considering the animal a new or different animal arose especially in analyzing the metabolism data on humans and has been treated in full by Benedict and Talbot (1921). The majority of the chimpanzees were studied in such short periods that no question of difference in age or weight occurs, and in these instances all the measurements at thermic neutrality for any one chimpanzee have been included in the general average.[7] In those instances in

[7] For Cuba all dates included in average except December 12, January 5, and January 10; for May all dates included in average except December 6 and February 5; for Mimi all dates included in average except February 28 and Mar. 13.

which considerable changes in age and weight occurred, two or more averages were made according to the changes in weight, as follows:

Al Data averaged for June 19 through July 6, 1934, inclusive.
Data averaged for May 13 through June 14, 1935, inclusive.

Bokar Data averaged for November 16, 1933, through March 14, 1934, inclusive.
Data averaged for June 20 and 25, 1935.

Gamma Data averaged for March 7 through June 12, 1934, inclusive.
Data for June 13, 1935, considered to represent a different animal.

Beta Data for March 9, 1934, considered to represent one animal.
Data averaged for May 7 through June 4, 1934.
Data for May 1, 1935, considered to represent a different animal.

Lia Data averaged for November 9, 1933, through March 15, 1934, except for November 9, January 16, and January 30.
Data averaged for March 30 through June 3, 1935, inclusive.

The average values for the basal metabolism of the chimpanzee, as outlined above, are summarized in table 10 according to increasing weights. Preference has been given to the arrangement of the data by increasing weights rather than by increasing ages, since the weights are precisely known in all cases whereas the ages are in many cases, particularly among the older chimpanzees, subject to some uncertainty. In general, animals are older as their weights increase, although animals of the same weight may at times have considerably different ages.

In comparative studies of the relation of such factors as age, weight, and sex, where different animals of the same species are to be compared, it is important that in the selection of the average values to be used in such comparisons there should be a most critical analysis of each individual observation. Consequently it is emphasized here again that all the experiments entering into these averages were those in which activity was completely ruled out and that any experiments made at temperatures below 20° C. were not included except in those two instances (Cuba and Bokar) when the lower temperatures were demonstrated not to have any effect upon the basal metabolism because the chimpanzees had become accustomed to the cold. As it has been proved that the zone of thermic neutrality of the chimpanzee is between 20° and 29° C., inclusion in the averages for the given animal of only the results obtained at thermic neutrality for that animal insures absence of the effect of environmental temperature in

TABLE 10

BASAL METABOLISM OF THE CHIMPANZEE

(Average values)

Chimpanzee	Number of days studied	Age		Body weight	Heat production per 24 hours		
					Total	Per kg.	Per 10 $w^{2/3}$
		yr.	mo.	kg.	cal.	cal.	cal.
Males							
Peter	1		2	2.94	226	76.8	1100
Peter	1		3	3.85	273	70.8	1108
Bob	3	1	2	4.92	296	60.6	1028
Don	2		11½	4.94	273	55.1	936
Dick	3	1	1	5.53	307	55.5	982
Tom	3	1	2	7.35	354	48.2	937
Al	3	[2]6		25.0	908	36.3	1061
Al[1]	5	[2]7		33.2	1085	32.7	1051
Bokar[1]	10	[2]9		37.1	1072	28.9	965
Bokar[1]	2	[2]10		48.1	1227	25.6	928
Females							
Rosy	2		11½	4.55	262	57.7	955
Helene	3	1	2	5.77	324	56.4	1010
Gamma	7	1	7	7.22	383	53.1	1025
Beta	1	2	4½	8.94	392	43.8	910
Beta	5	2	6½	9.96	486	48.8	1049
Gamma	1	2	8½	12.0	450	37.5	858
Beta	1	3	6	14.2	513	36.1	873
Gua	3	2	11½	14.9	517	34.9	856
Mamo	3	[2]6		21.1	762	36.2	1000
Soda	4	[2]7		24.7	865	35.0	1019
Bentia	4	[2]8		27.3	857	31.5	946
Cuba[1]	10	7	9½	31.2	1026	33.0	1037
May[1]	9	[2]9		32.2	1072	33.3	1059
Lia[1]	12	[2]10		33.0	1048	31.9	1020
Lia[1]	5	[2]11		33.5	994	29.7	956
Wendy[1]	42	[2]11		35.2	1008	28.7	939
Josie[1]	39	[2]13		39.3	1082	27.5	936
Pati[1]	6	[2]15		44.9	1154	25.7	913
Mimi[1]	6	[2]11		46.4	1387	29.9	1076

[1] Adult.

Estimated age.

the comparisons. With the data in table 10 thus classified, it is now possible to study by comparison of the different chimpanzees the relation of such factors as size, age, and sex, and to compare the basal metabolism of the chimpanzee with that of animals of other species.

COMPARISON OF DATA OBTAINED ON NEW HAVEN AND ORANGE PARK CHIMPANZEES

The values obtained by Bruhn (1934) for the metabolism of three adolescent male chimpanzees living in New Haven are recalculated on the basis of 10 $w^{2/3}$ in table 11. These values are from 19 to 23 per

TABLE 11

BASAL METABOLISM OF NORMAL ADOLESCENT CHIMPANZEES AT NEW HAVEN[1]

Body weight	Chamber temp.	R.Q.	Heat production per 24 hours		
			Total	Per kg.	Per 10 $w^{2/3}$
kg.	°C.		cal.	cal.	cal.
14.1	23.0	0.82		32.0	
	22.9	.79		34.9	
	23.1	.83		34.4	
Average	23.0	.81	476.6	33.8	817
16.4	22.9	.80		31.8	
	23.5	.75		32.8	
	23.3	.78		36.3	
	22.8	.79		32.7	
Average	23.1	.78	547.8	33.4	849
24.5	25.5	.80		30.2	
	23.6	.79		28.9	
	23.5	.85		29.3	
Average	24.2	.81	722.7	29.5	857

[1] Twelve hours without food, asleep at night. (Bruhn, 1934.)

cent lower than values obtained upon the male Al at Orange Park. The reason for this difference is not immediately obvious but may be accounted for in part at least by the dissimilarity in the living conditions of the animals at New Haven and Orange Park. The animals

at New Haven were confined for the greater part of the year and especially during the winter months, when the observations were made, to small indoor cages where exposure to sun was practically eliminated and where there was little or no chance for exercise. The environmental temperature was without significant changes, as the chimpanzees were kept inside of rooms the temperature of which was fairly constant. These living conditions are in marked contrast to the environment at Orange Park, where each animal has access to a rather large outdoor cage with much greater freedom of movement, and where even during winter months the animal is exposed to the sun. The animals at Orange Park are subjected by choice to greater variations in temperature, as they are not confined at any time to the warm inside living quarters. The entire environment at Orange Park can be considered more stimulating and more normal than that at New Haven. Hence it is believed that the values obtained on the Orange Park animals represent a metabolism on a higher and more normal plane than the figures for the New Haven animals.

Size

Total heat production referred to body weight.—During the growth of an animal one expects great changes in size. In comparisons of the metabolism of young growing animals, therefore, the factor of size inevitably plays a role. This factor is also present in comparisons of adults, for not all adults of the same species are of the same size. Examination of the data in tables 3 to 9 for those chimpanzees that were studied over a period of time characterized by a marked change in body weight shows that as the body weight increased, the total metabolism also increased. Thus, with the year-old chimpanzee Ben, an increase in weight from 4.8 to 7.8 kg. was accompanied by an increase in total heat production from 210 calories to 358 calories. Gamma, when weighing about 7 kg. (1 year old), had a total heat production of approximately 400 calories and when weighing 12 kg. (nearly 3 years old) but 450 calories. Similarly with Beta at a weight of 9 kg. (2 years old) the metabolism was 392 calories and at a weight of 14 kg. (3½ years old) it was 513 calories. Al, at a weight of 25 kg. (6 years old), had a heat production of 858 calories and at a weight of 33 kg. (7 years old) nearly 1,100 calories. The older chimpanzee Bokar (9 to 10 years old), with a change in weight from 37 to 48 kg., showed a smaller change in total heat production, namely, from 1,100 to but 1,200 calories. Examination of the average values for each individual chimpanzee given in table 10 shows, as is to be expected,

that the large chimpanzees have a large total heat production and the smaller chimpanzees a smaller total heat production. This is illustrated graphically by the lowest curve in figure 5, in which the average total 24-hour heat production of each chimpanzee has been plotted with reference to the body weight. A curve has been drawn through the plotted data to indicate the general trend of the values. Here one sees clearly that with the increasing body weight there is an increasing total heat production.

Heat production per kilogram of body weight referred to weight.—Although the smaller animal has the smaller total metabolism, it is well known that among animals of the same species the smaller has the larger heat production per kilogram of body weight. That this is also true of the chimpanzee is shown by the middle curve in figure 5, which represents the trend of the average heat production per kilogram of body weight of the individual chimpanzees referred to their respective body weights. The curve in this instance is at a high level at the start, but falls off rapidly and tends to flatten out at the higher weights.

Heat production referred to the two-thirds power of the body weight.—In the uppermost part of figure 5 have been plotted with reference to the body weight the average values for the heat production per 10 $w^{2/3}$. Although there are two high values at weights under 5 kg., there is no distinct tendency for the metabolism per 10 $w^{2/3}$ of the 5-kg. chimpanzees to be any higher than that of the chimpanzees weighing nearly ten times as much. This is contrary to the trend noted with humans, whose metabolism per unit of surface area is low at 3 kg., increases rapidly with increasing weights up to 10 or 12 kg., and thereafter decreases till it reaches almost a uniform level at weights above 50 kg. (See figure 6, page 315.)

Age

The relation of age *per se* and metabolism can best be studied by a long series of experiments upon one and the same animal from birth to adolescence and, indeed, to old age, but for obvious reasons no such study has ever been made or even initiated. Experience with humans, based in several instances upon a fairly long series of observations on one and the same individual, but in greater part upon scattered observations on many individuals of greatly differing ages, shows that there is a decided tendency for a lessened metabolism with old age. Therefore, it is of interest to determine whether this is also true of the chimpanzee. As our observations did not include measurements on

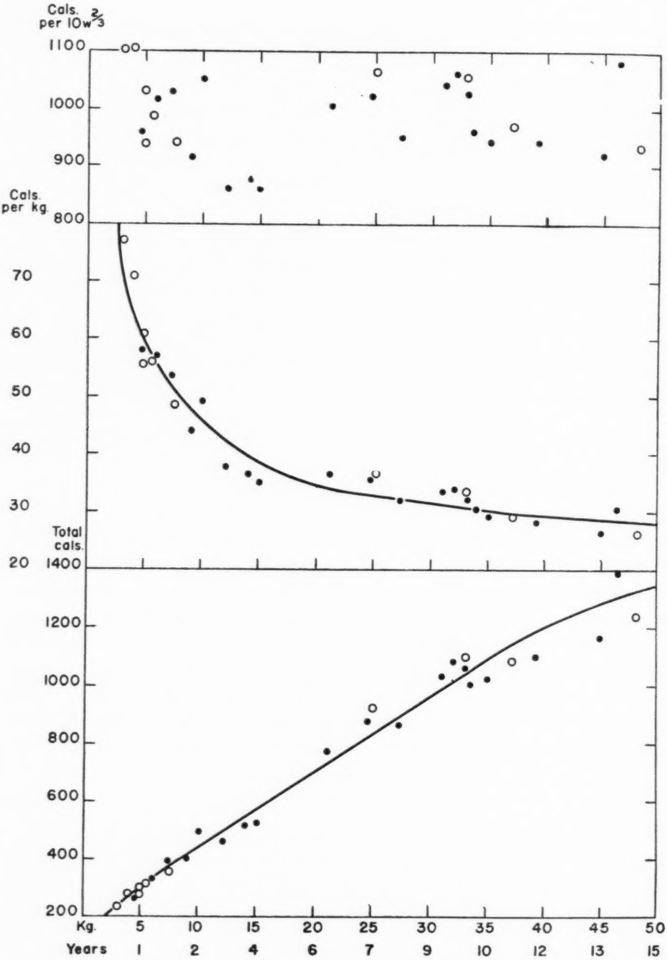

FIGURE 5. Basal heat production of the chimpanzee referred to body weight and age.

The males are indicated by the hollow circles and the females by the solid dots. The plotted data in the lowest section of the chart represent the total 24-hour heat production, those in the middle section the heat production per kilogram of body weight, and those in the top section the heat production per 10 $w^{2/3}$. The abscissae indicate the actual body weights and the approximate ages corresponding to the weights.

one and the same chimpanzee from infancy to adult or old age, our only recourse is to analyze the metabolism data obtained upon the several chimpanzees with reference to their ages and note whether the age factor is dominant in any way. As can be seen from table 10, the youngest age was 2 months and the oldest 15 years, and no chimpanzees were studied between the ages of 3½ and 6 years. Inasmuch as age is so closely correlated with body weight, particularly during the period of growth, it is unnecessary to plot the chimpanzee data specifically with reference to age. It has been considered sufficient to indicate in figure 5 the approximate ages corresponding to the body weights represented by the abscissae.

Examination of the lowest curve in figure 5 shows that the total heat production of the chimpanzee increases with age but that at ages of 10 years and over it tends to become more uniform at about 1,000 or 1,100 calories.

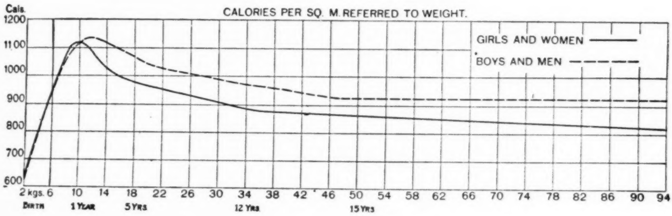

FIGURE 6. Basal heat production of humans per square meter of body surface per twenty-four hours referred to age and to body weight.

For comparison with the chimpanzee data in the uppermost section of figure 5, the previously published curves (Benedict, 1928) for the 24-hour heat production per square meter of body surface of humans from birth to adult life are reproduced in figure 6. Among humans the child shows the greatest intensity of metabolism at the age of one year, not only per kilogram of body weight but likewise per unit of surface area. From comparisons of the metabolism of other animals of various sizes in any given species, one would expect that the child, being small, would have a higher metabolism per unit of weight than the adult, but the child likewise has a higher heat production per unit of surface area. Only one chimpanzee appreciably under one year of age was studied, but several were measured when about one year old. The chimpanzee, like the human, has a high metabolism per unit of weight in early youth and a lower metabolism at the adult ages,

but in striking contrast to the human the chimpanzee has a metabolism expressed per two-thirds power of the body weight that is not specifically higher in early youth than in adult life.

At all body weights and at all ages (as can be seen from figure 5) the heat production of the chimpanzee per 10 $w^{2/3}$ or, as it is ordinarily called, per square meter of body surface, is remarkably uniform. On the average for all the chimpanzees it is 980 calories. This, at first sight, seems to be a striking confirmation of Rubner's thesis that the heat production of all warm-blooded animals is the same per square meter of body surface independent of size. But this uniformity in the case of the chimpanzee obtains not only with the adult chimpanzees weighing 20 kg. or over but also with the young chimpanzees. Although Rubner's experiments which, he claimed, emphasized the uniformity of the heat loss or heat production per unit of surface area were, for the most part, made on adult animals, he and Heubner and others subsequently extended their observations to include the very early ages and assumed that the surface area law likewise held in early youth. At the present date, owing to the large number of metabolism measurements made on infants, all writers can agree that at the younger ages the metabolism per unit of surface area is higher than that in later years. This factor of age, as such, was not emphasized by Rubner in formulating his surface area law, but is now recognized by all workers in metabolism. To be sure, the chimpanzees represent a much more homogeneous group than the humans who have been studied, so far as living conditions, environmental temperature, and diet are concerned, and doubtless the effect of the age factor in the case of the chimpanzee is masked by the effect of the changes in body weight.

Another fact that militates against the use of the data for the chimpanzee as a support for the body surface law is only too rarely recognized by advocates of this law. Rubner's value of 1,000 calories per square meter of body surface per 24 hours was based upon measurements on animals at 16° C., but Rubner stated in 1931 that if the measurements were made at 30° C. the heat production per unit of body surface would be more nearly 615 calories. It remains a fact that with the chimpanzee, at least, the age factor as such is not evident in the heat production per 10 $w^{2/3}$ (*i.e.*, per square meter of body surface) at the younger ages, and that throughout the entire age range from 2 months to 15 years these animals, as a whole, irrespective of weight and irrespective of age, have a metabolism of 980 calories per 10 $w^{2/3}$. This whole story of the influence of age upon metabolism

and its accompanying inevitable factor, size or weight, demands further investigation, particularly with animals. In the two series of observations made by the Nutrition Laboratory on rats in two different colonies (Benedict and MacLeod, 1929; Horst, Mendel, and Benedict, 1934a, 1934b) the picture obtained is by no means clear, and the effect of age is nowhere near so striking as that noted with humans.

Sex

With humans it has been found that the basal metabolism of women is approximately 7 per cent below that of men (Gephart and Du Bois, 1916; Harris and Benedict, 1919). With rats also the metabolism is lower in the female than in the male (Horst *et al.*, 1934a, 1934b). Because of the great variability in the sizes of the chimpanzees studied obviously no one figure can be given to represent the heat production comparable, for example, to that of one calorie per kilogram of body weight per hour typical of the basal heat production of the average adult man. Inspection of the data in table 10 shows that the adult female chimpanzee in good nutritive condition, in the weight range from 32 to 46 kg., weighs on the average about 38 kg. From the curve in figure 5 drawn through the plotted points for the total 24-hour heat production referred to body weight, it can be seen that the total metabolism of the 38-kg. chimpanzee would be about 1,140 calories. One female chimpanzee at Orange Park, Mona, weighs 85 kg. She would be classed as comparable to an excessively fat woman. Although her metabolism was not measured, obviously it would be considerably greater than the 1,140 calories ascribable to the average female chimpanzee weighing 38 kg.

Our data on the average adult male chimpanzees are unfortunately limited to two animals, Al and Bokar. Each of these animals underwent a relatively small increase in body weight during the period of experimentation and fortunately a number of experiments (although far too few) were made with each at each new weight level. These adult males had not reached their maximum weight at the time of our observations. It is estimated that the average adult male chimpanzee at Orange Park would weigh not far from 54 kg. The curve for total heat production in figure 5 is not carried beyond 50 kg., but if it were projected beyond this weight it can be seen that at 54 kg. the total heat production would average about 1,320 calories per day. Here is encountered immediately the difficulty of comparing an adult 38-kg. female chimpanzee having a total heat production of 1,140 calories with an adult 54-kg. male chimpanzee having a probable total heat

production of 1,320 calories. The larger animal would obviously have the larger heat production. The body weight of the male is 42 per cent greater than that of the female, but the total heat production is only 16 per cent greater. Off hand it would appear that the intensity of the metabolism was higher in the female. The comparison on the basis of these estimated averages is by no means conclusive. We are then left face to face with the problem that we must study the basal metabolism of each animal and select, if possible, an *average* figure that would be representative of this particular animal.

Another method of comparing the metabolism of the adult male and female chimpanzees, which vary so in weight, is on the basis of the heat production per unit of weight or per two-thirds power of the body weight. It has already been emphasized that the expression of the heat production per unit of weight does not wholly equalize the differences in weight, since the smaller the animal, the greater the heat production per kilogram of body weight. If the heat values per kilogram of body weight of male and female chimpanzees of the same body weights are compared, one might expect to find in general a difference due to sex, *i.e.*, that the metabolism of the males is either above or below that of the females. Inspection of the plotted data in the middle section of figure 5, however, indicates that there is no specific tendency for the males (indicated by the hollow circles) to be above or below the curve representing the general trend of the values. Indeed, if two curves were drawn, one through the plotted data for the males alone and one through those for the females alone (indicated by the solid dots), they would, for the greater part, at any given weight be superimposed. There is no suggestion that the metabolism of the males is, on the whole, above that of the females, although occasionally, notably at 25 kg., the circle for the male stands out as being above the dot for the female. On this basis of comparison, however, the evidence in general is against any sex difference in metabolism. This, again, is contrary to the experience with humans. Similarly, in the uppermost section of figure 5, where the data are plotted on the basis of the heat production per two-thirds power of the weight, there is no suggestion of the slightest difference in the metabolic levels of the two sexes.

From the Nutrition Laboratory's experience with man, a difference in the metabolism of males and females is not to be expected at the early ages, but after adolescence there is a striking difference of ca. 7 per cent between the metabolism of men and women. With rats there is a difference between the metabolism of males and females, both at

the young and adult ages, the males having the higher heat production. Although the observations on the chimpanzees suggest that there is no sex difference in metabolism at any age, further data are needed before any definite conclusion can be drawn. At present too few adult males have been studied. Nearly an equal number of observations have been made on each sex at the youthful ages and these show, as has been noted with humans, that there is no clear difference in the metabolism of males and females up to about three years of age.

Energy intake compared with probable energy needs

A 3-day study (not consecutive) of the food consumption of the adult chimpanzee indicates that the average energy intake amounts to 2,900 calories per day. This is based upon the average food intake of about twenty adult chimpanzees, most of them females. As the adult female would average only a little less than 40 kg., the average weight for the entire group in this digestion study can be considered to be approximately 40 kg. Since no significant difference has been noted in the metabolism of the males and females of these higher weights, it can be assumed that the basal total heat production of an average chimpanzee weighing 40 kg. would be 1,200 calories. Correction of this value for the influence of sleep (which with man depresses the metabolism about 10 per cent) would give a basal value of approximately 1,330 calories per 24 hours. Thus the energy intake of 2,900 calories would be 118 per cent above the minimum energy requirements. The average adult man of 60 kg. has a probable total basal heat production of 1,440 calories per 24 hours (on the basis of a heat production of one calorie per kilogram of body weight per hour). If this is increased by 118 per cent, the probable energy intake would be 3,140 calories. As the average chimpanzee would weigh but two-thirds the weight of the average man, its probable energy intake (if represented by two-thirds of the energy intake of man) would be about 2,100 calories as compared with the 2,900 calories noted in the 3-day digestion study. The actual intake of 2,900 calories, therefore, seems very high. As no productive work is engaged in by the chimpanzee comparable at all to that of the ordinary American laborer either at moderate or severe muscular work, and as these animals do not, except in rare instances, continuously take on weight, it is clear that this energy obtained in the food must be expended in exercise and that the cage activity of the adult chimpanzee is such as to call for a very heavy expenditure of energy.

Comparison of the Basal Metabolism of the Chimpanzee and Man

The dominant note in this study of the chimpanzee has been to secure information regarding an infrahuman primate for ultimate association with observations on man. Hence in summarizing the results of our measurements on the chimpanzee discussed in the foregoing pages, we think it opportune to compare the basal metabolism of the chimpanzee with that of the human subject.

The post-absorptive condition is reached by both chimpanzee and man after 12 hours of fasting, when the respiratory quotient reaches a level of approximately 0.82.

Emotional excitement increases the metabolism of both, but the chimpanzee, like man, can adjust itself readily to the experimental technique of respiration experiments without a long period of training.

The zone of thermic neutrality is probably much the same with both human subjects and chimpanzees, namely from 20° to 29° C., and in the case of chimpanzees inured to cold may extend to as low as 17° C. The amount of hair protection plays no role with the chimpanzee at temperatures between 20° and 29° C.

The variability in the metabolism of the chimpanzee from day to day or week to week is greater than that to be expected with well-conditioned human subjects. In studies of the effect of any superimposed subtle factor, therefore, the basal metabolism of the chimpanzee should be determined *immediately before* the measurement of the metabolism under the special superimposed condition. Knowledge of the average basal metabolism of the chimpanzee is of value only in general comparisons of this animal's metabolism with that of another chimpanzee.

Season has no sharply defined uniform effect with either the chimpanzee or man.

The age of maturity of the chimpanzee (about 8 years) and of the elephant (about 10 to 12 years) more nearly approaches that of humans than is the case with any other animal species.

With both the chimpanzee and woman a variable effect of menstruation may be expected. In some instances the metabolism may be depressed during menstruation and elevated on intermenstrual days. In other instances it may be depressed on intermenstrual days and higher during the menstrual period itself.

Size plays the same role with the chimpanzee as with man, that is, the larger the chimpanzee, the greater the total heat production, and the smaller the heat production per kilogram of body weight. The heat production per 10 $w^{2/3}$, however, is fairly uniform at all body

weights contrary to that of humans which is higher at 10 or 12 kg. (1 year) than at the larger weights.

The total heat production increases continually from youth to adult age with the chimpanzee as well as with man. Both species have a high metabolism per unit of body weight in early youth and a lower metabolism at the adult ages. In striking contrast to man, however, who has a higher heat production per unit of surface area during youth than during adult life, the chimpanzee has a metabolism expressed on this basis that is essentially the same at all ages. Owing to the great difference in the sizes of young and adult chimpanzees, whose body weights vary from about 2 to 40 kg., and owing to the fact that adult animals of other species have, as a whole, a lower heat production per 10 $w^{2/3}$ the lower the body weight, it is clear that in the case of the chimpanzee the stimulus to metabolism of youth and early maturity is particularly pronounced, indeed offsetting the expected lower heat production per 10 $w^{2/3}$ of animals at the smaller weights (smaller areas). That the adjustment between the effects of these two factors, size (area) and youth, is such as to bring the heat production per 10 $w^{2/3}$ to a uniform level at all ages and weights is, to say the least, remarkable. There could be no more striking confirmation of Rubner's surface area law than these observations, taken by themselves. Furthermore these results are quite in harmony with Rubner's original series on dogs, ranging in weight from 3 to 31 kg. On the other hand, the extensive metabolic survey made by the Nutrition Laboratory with animals of widely different species shows that this uniformity in metabolism per 10 $w^{2/3}$, which appears definitely with the chimpanzee and in all probability with the dog, is by no means general. In fact, these two species of animals may be considered to represent the striking exceptions.

In general the chimpanzees, unlike man, show no sex difference in metabolism, but the data with chimpanzees are too few to draw any definite conclusions.

The basal heat production of the adult chimpanzee is, on the average, 980 calories per two-thirds power of the body weight (times 10), or approximately the same as that of man per unit of surface area.

Problems remaining to be solved

It is fully realized that there are many aspects of the energy metabolism of the chimpanzee which for various reasons could not be investigated. It was a question of what would be the most important findings obtainable in the length of time at our disposal. Without any thought

of preempting the field we offer certain problems, some of which would contribute importantly to our discussion, and others of which are of considerable interest to both the comparative physiologist and those research workers selecting an animal for experimentation.

Necessarily our observations have been limited in some phases by the unavailability of animals. It is not common practice at the station to separate an infant chimpanzee from its mother before it is one year of age. Therefore, the number of animals studied under one year of age has been small; in fact, only one animal was studied. In the future as very young infants become available, they should be studied.

In view of the adult male's dislike at being confined in the metabolism chamber and his destructiveness, it has not been found practicable to study more than one mature adult male. The reason for this animal's (Bokar) tractability has been given. It is highly desirable and entirely possible in the future to study the metabolism of adult male and female chimpanzees and further the comparison.

The metabolism of the pregnant chimpanzee has been barely touched upon but deserves considerable study.

A study of prolonged fasting in the chimpanzee similar to that made on man (Benedict, 1915) would be highly desirable.

The metabolism of the same chimpanzee from infancy to maturity or old age should serve to clarify a picture which at present is a composite made up of studies of many animals of varying ages.

In view of the eating habits of these animals a study of the effect of ingested food on heat production is of considerable importance. Such a study should include determinations of the "specific dynamic action," the "respiratory quotient," and the rate of passage of food through the intestinal canal.

In connection with the study of the metabolism of infancy, information on the composition of the milk of the chimpanzee and the amounts the infant obtains in twenty-four hours is particularly desirable.

Studies of the heart rate under various conditions (during sleep and during muscular activity), supplemented by electrocardiograms, are highly desirable.

Finally, but certainly not completing the list of promising lines of research on the chimpanzee, temperature (rectal, vaginal, and skin) studies are desirable. Temperature studies are now being carried out at the Orange Park laboratory.

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